



## CO-EDITORS

Lesley J. Rogers  
Prof. of Neurosci. & Animal Behaviour  
School of Biological Sciences  
University of New England  
Armidale NSW 2351  
AUSTRALIA

Sally A. McFadden  
Dept. of Psychology  
The University of Newcastle  
NSW 2308  
AUSTRALIA

## ASSOCIATE EDITOR

Nancy K. Innis  
Dept. of Psychology  
University of Western Ontario  
London, Ontario, N6A 5C2 Canada

## EDITORIAL ADVISORY BOARD

Ruben Ardila  
University of Colombia  
Apartado 88754  
Bogota Colombia S.A.

Juan D. Delius  
Allgemeine Psychologie  
Universitat Konstanz  
D-78434 Konstanz 1  
GERMANY

Jack Demarest  
Department of Psychology  
Monmouth University  
West Long Branch  
NJ 07764, USA

Gordon G. Gallup Jr  
Department of Psychology  
SUNY at Albany  
Albany, NY 12222 USA

Gary Greenberg  
Dept. of Psychology  
Wichita State University  
Wichita, Kansas  
67260-0034 USA

R. Bryan Jones  
Roslin Institute  
(Edinburgh), Roslin  
Midlothian EH25 9PS  
SCOTLAND

Peter Klopfer  
Department of Zoology  
Duke University, Durham  
NC 27706 USA

Mauricio R. Papini  
Department of Psychology  
Texas Christian University  
Fort Worth, TX 76129 USA

Wojciech Pisula  
Faculty of Psychology  
University of Warsaw,  
Stawki 5/7  
00-183 Warsaw POLAND

Emanuela Prato Previde  
Istituto di Psicologia della  
Facolta Medica  
Universita di Milano, via T.  
Pini 1  
20134 Milano, ITALY

Michael Renner  
Department of Psychology  
West Chester University,  
West Chester  
PA 19383 USA

Leickness C. Simbayi  
Department of Psychology  
University of Fort Hare  
Private Bag X1314  
Alice 5700, SOUTH  
AFRICA

Roger K. Thomas  
Department of Psychology  
The University of Georgia,  
Athens  
GA 30602-3013, USA

Ethel Tobach  
American Museum of  
Natural History  
Central Park West at 79th St  
New York 10024-5192,  
USA

Dora F. Ventura  
Instituto de Psicologia  
University of Sao Paulo,  
Cx. Postal  
Sao Paulo, BRAZIL

Jeannette P. Ward  
Department of Psychology  
The University of Memphis  
Memphis, TN 38152 USA

# INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY

Volume 11, Number 2, 1998

---

## **IXth Biennial Meeting of the International Society for Comparative Psychology, September 1-5, 1998**

<i>Introduction</i>	41
<i>Abstracts</i>	43

## **The Napoli Social Learning Conference, June 30 - July 5, 1998**

<i>Introduction by C.M. Heyes and B.G. Galef, Jr.</i>	73
<i>Abstracts</i>	77

**INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY** is sponsored by the International Society for Comparative Psychology, an affiliate of the International Union of Psychological Sciences. In consonance with the goals and activities of the Society, it publishes reports of studies in the evolution and development of behavior of all species; on the use of the comparative method for the understanding of behavioral processes; and the examination of the adequacy of psychological and evolutionary theories. It accepts articles that deal with historical and contemporary relationships between humans and other animals; that elucidate problems of ecological and behavioral processes in resource management; that explicate fundamental concepts about human evolution; and that present research results and develop theories about the development and evolution of behavior. Articles on the contemporary and historical organization of knowledge about comparative psychology; promoting public education on the evolution and development of behavior; and about the training of students in comparative psychology are also invited. Book reviews; letters discussing published articles with replies by authors; notices of new books, journals, meetings and competitions or other matters of interest to the readers will be published at the discretion of the editors. The Editors and Associate Editor are elected by the Operations Committee of the Society. The Editorial Advisory Board is appointed by the Editors and the Operations Committee.

**MANUSCRIPTS** should be submitted in triplicate to the Editors. See inside back cover for style requirements.

**SUBSCRIPTION** inquiries and subscription orders to institutions and individuals who are not Society members should be addressed to International Society for Comparative Psychology, P.O. Box 1897, Lawrence, KS 66044-8897, USA, Telephone 913-843-1221, or Fax 913-843-1274. Subscription inquiries and subscription orders for Society members should be addressed to Professor Robert M. Murphey, Secretary, International Society for Comparative Psychology, Department of Psychology, University of California, One Shields Ave., Davis, California 95616-8686 U.S.A.. Telephone: (530) 752-1855; Fax: (530) 752-2087.

*Subscription rates:*

Volume 11, 1998 (4 issues) \$95.00 (outside the U.S., \$110.00). Members of the International Society for Comparative Psychology receive their yearly subscription as part of their membership dues. For membership information see back pages.

**INDEXED OR ABSTRACTED IN:** Psychological Abstracts.

**PHOTOCOPYING:** Authorizations to photocopy items for internal and personal use of specified clients is granted by the International Society for Comparative Psychology for users registered with the Copyright Clearance Center (CCC) Transactional Reporting Service, provided that the flat fee of \$6.50 per copy per article (no additional per-page fees) is paid directly to CCC, 27 Congress St., Salem, MA 01970. For those organizations which have been granted a photocopy license by CCC, a separate system of payment has been arranged. The fee code for users of the Transactional Reporting Service is: 0889-3667/91/\$6.50.

**COPYRIGHT** 1998/1999 by the International Society for Comparative Psychology. Published quarterly.

IXth BIENNIAL MEETING OF THE  
INTERNATIONAL SOCIETY FOR  
COMPARATIVE PSYCHOLOGY  
*September 1-5, 1998, South African Museum,  
Capetown, SOUTH AFRICA*

**INTRODUCTION**

The ninth biennial meeting of the International Society for Comparative Psychology was held at the South African Natural History Museum, which was a most appropriate venue in light of the nature of our opening sessions. These first presentations discussed the natural history of South Africa, the anthropological roots of South African peoples, paleogeography, evolutionary history, and the behaviour of the native fauna. This has become the signature practice of our biennial meetings.

As at previous meetings which have also been held in interesting places including Mexico, Costa Rica, Barbados, Australia, Belgium, Brazil and Canada, the program was noteworthy for not just the international representation of the speakers, but the associated breadth of species, topics and applications and indeed comparative approaches intrinsic to the international nature of our speakers. Theories, ideas and empirical data were met with open and vigorous discussion from rich and varied perspectives.

From Presidential addresses, to keynote speakers, to symposia, and to individual presentations, the meeting was characterized by high quality scientific work and open discussion. Allen Gardner, the outgoing President, discussed chimpanzee language and cognitive capabilities and we were treated to some historical filmed footage of the now famous Washoe in the early stages of her linguistic training. Ethel

---

Address enquiries to Jeannette Ward, President ISCP, Psychology Department, University of Memphis, Memphis, Tennessee 38152 USA or Gary Greenberg, President Elect ISCP, Psychology Department, Wichita State University, Wichita, Kansas 67260 USA.

Tobach spoke to the future of comparative psychology and identified new roles and challenges for the field in the 21<sup>st</sup> century.

As you would expect from the comparative approach, the abstracts of papers printed in the following pages cover a range of species: including grain beetles and spiders, pigeons, chickens and quail, and rats, dolphin, primates and humans, and deal with the complexity of behaviour, from web building by spiders, dust bathing and aggression in chickens, vision and learning in laboratory reared animals, and cognition in dolphins, chimpanzees and early man.

The full program of the meeting is available in our Newsletter, Volume 15, No. 1, March, 1999. We are certain you will gain a true appreciation of the nature of the ISCP from reading these varied abstracts from our program. We welcome you to join us at our next meeting in Warsaw, Poland in July, 2000.

IXth BIENNIAL MEETING OF THE  
INTERNATIONAL SOCIETY FOR  
COMPARATIVE PSYCHOLOGY  
*September 1-5, 1998, South African Museum,  
Capetown, SOUTH AFRICA*

**ABSTRACTS OF PAPERS**

THE EFFECT OF PESTICIDES ON LEARNING IN THE AFRICANIZED HONEY BEE. *Charles I. Abramson, Department of Psychology, Oklahoma State University, U.S.A.*

The purpose of the experiment is to examine the behavioural effects of four popular insecticides used to control the cotton boll weevil in Brazil on the learning ability of the Africanized honey bee (*Apis mellifera* L.). There was interest as well in determining whether classical conditioning of proboscis extension can be used as a bioassay in the Africanized honey bee. In a series of experiments, the classical conditioning of proboscis extension in harnessed forager was used to investigate the ability of these pesticides to function as signals and rewards. The results indicated that: 1) The odours of Sevin, Baytroid, Endosofan, and Decis are not repellent to bees and such odours can serve as cues to a food source, 2) When placed in a sucrose solution, bees readily consume all four pesticide, 3) Learning can occur when the unconditioned stimulus consists of a compound of pesticide and sucrose, 4) Prefeeding with Sevin, and Baytroid 1 hour before the experiment produces high mortality rates, less so with Endosofan, and no mortality with Decis, 5) Prefeeding with Decis does not interfere with learning. The results are discussed in terms of the need to limit pesticide use.

---

Abstracts are listed alphabetically by first author. Address any correspondence about the meeting to the Chair of the Local Organising Committee; Prof. L. Simbayi, Department of Psychology, University of the Western Cape, Private Bag X17, Bellville 7535, Cape Town, South Africa. E-mail: [LSIMBAYI@uwc.ac.za](mailto:LSIMBAYI@uwc.ac.za)

THE EFFECT OF ETHANOL ON EUROPEAN HONEY BEES (*APIS MELLIFERA* L.). Charles I. Abramson, *Department of Psychology, Oklahoma State University, U.S.A.*

A series of experiments were performed to test the feasibility of creating a animal model of alcoholism using social insects. The honey bee was selected as the first social insect to be tested because much is known about its natural history, physiology, genetics, and behaviour. Moreover, they are inexpensive to procure and maintain. Of special interest is their use of "language," communication "skills" and social organization. As a necessary first step, studies were conducted to determine whether honey bees will consume alcohol, and its effect on behaviour. The results indicated that: 1) Honey bees will readily consume a 1%, 5%, 10% and 20% alcohol solution, 2) The amount consumed of each solution does not differ in terms of either amount consumed or contact time from a 1.8 M sucrose control, 3) Previous exposure to a lesser concentration of alcohol does not influence consumption of a higher concentration (no contrast effect) 4) Under special conditions honey bees will readily drink 95% ethanol, 5) Consuming a 10% or 20% solution impairs learning as measured by proboscis extension, and locomotive behaviour as measured in both a shuttlebox and running wheel. Exposure to ethanol did not influence stopping behaviour.

HAND PREFERENCES IN LION TAMARINS *LEONTOPITHECUS CHRYSOMELAS* AND *L. CHRYSOPYGUS*: EFFECTS OF DIFFERENT POSTURAL DEMANDS. Cesar Ades and Vania Haddad Diego, *Institute of Psychology, University of Sao Paulo, Brazil.*

There is almost no information about hand preferences in lion tamarins (Singer & Schwibbe, 1997). The purpose of our study was to investigate hand use when reaching for food in two species of lion tamarins (*L. chrysomelas* and *L. chrysopygus*), in tasks differing in postural demands. Parcels of food were offered to adult individuals (1) when the animals were suspended on the wire mesh of their cages, extending out one the forelimbs (15 *L. chrysomelas*; 19 *L. chrysopygus*); (2) on a horizontal platform (16 *L. chrysomelas*; 14 *L. chrysopygus*). There were no differences between species or between genders in both tasks. In task 1, a significant population bias towards right handedness was found; 25 individuals were right-hand preferent, 2 were left-hand preferent and 7 were ambipreferent. In task 2, however, there was a symmetrical distribution of hand preferences at the population level, with 11 right handed, 14 left handed and 5



ambipreferent individuals. Difference in the distribution of left and right preferences between tasks 1 and 2 was significant. 10 of the right-hand preferent individuals of task 1 switched their preference to the left hand when reaching for food in task 2. When tested again in task 1, most of such individuals reverted to preferential use of the right hand. Results indicate that both *L. chrysomelas* and *L. chrysopygus* can display a consistent preference for right hand use, as do tamarins *Saguinus oedipus* (King, 1995), but that this preference is task-dependent and is influenced by postural demands. Switching in hand preferences at the individual level according to task is an intriguing feature of the results which deserve further investigation.

**MODULAR AND FLEXIBLE ASPECTS OF WEB DEVELOPMENT IN A GIANT ORBWEAVER.** *Cesar Ades and Hilton Japyassu, Institute of Psychology, University of Sao Paulo, Brazil.*

The study of marked changes during ontogeny provides a particularly good opportunity for understanding organization and re-organization of behaviour items. Here we examine one of such interesting cases, the transition in web-building of the giant, tropical spider *Nephilengys cruentata* from initial, perfect orbs to the incomplete, semi-orbs of later stages of life, under normal conditions and under different environmental constraints. Two types of ontogenetic processes were identified in normal growth: global increases in size and gradual, quadratic-type suppression of upper components of the web. Upper web parameters showed turning points (passage from increasing to decreasing trends) which were not simultaneous and which clustered into two transitional periods. Results of this first study indicate that changes in different parts of the web are governed by different ontogenetic rules. In a second study, performed with groups of spiderlings kept under different diets, rate of web development was shown to be related to feeding rate: poorly fed spiders had lower weights and slower web growth but nonetheless kept the global size of their web constant. Investment in foraging was thus privileged relatively to investment in body growth. In a third study, we manipulated the geometry of the frames offered to growing up spiders. In semi-circular frames, devoid of corners and vertical discontinuities, spiders increased environmental exploration and delayed the building of the first web, when compared to spiders in square and U-shaped types of frames. Frame geometry, which did not influence the first transition from orb to semi-orb webs, did however affect the frequency of regressive events and the timing of attainment of stable building

strategies. Taken as a whole, our results reinforce a modular and flexible conception of web development and have evolutionary implications: developmental uncoupling between ontogenetic algorithms opens, at the evolutionary level, the possibility of structural novelties in web building.

**IS FEATHER PECKING IN LAYING HENS ASSOCIATED WITH PECKING AT INANIMATE OBJECTS?** *Caroline E. Channing, Paul M. Hocking and R. Bryan Jones, Division of Environment and Welfare, Roslin Institute, Scotland, U.K.*

Feather pecking (FP) is one of the major obstacles to the widespread adoption of putative welfare-friendly systems for housing poultry, such as free range. As part of an attempt to identify behavioural traits associated with FP, the present study focussed on pecking at a variety of objects in adult laying hens that were characterised as either "peckers" (P) or non-peckers (NP). Peckers were survivors with good plumage from groups in which FP-related deaths had occurred; non-peckers also had good plumage but came from groups with no beak-related damage. The 16 hens were housed individually as pseudo-pairs (1 P and 1 NP bird in adjacent battery cages). At 33 weeks of age we measured their pecking responses when the following objects were suspended vertically from the top of the cage for 5 min : Day 1 = a bunch of conspecific feathers, Day 2 = bunches of feathers or string presented simultaneously, Day 3 = 2 differently coloured buttons, Day 4 = 2 differently coloured bunches of string. The P hens pecked significantly sooner and more often than NP ones at string and buttons and showed a similar numerical trend when presented with bunches of feathers. Furthermore, whereas all P hens pecked the buttons, 4 NP ones failed to do so. Though we must exercise caution in extrapolating from small data sets, these findings suggest that FP may be associated with increased motivation to peck at any object regardless of its nature.

**BILATERAL ARCHISTRIATAL LESIONS IN JAPANESE QUAIL CHICKS IMPAIR ADULT FEAR BEHAVIOUR.** *D. Ceri Davies<sup>1</sup> and Andrew D. Mills<sup>2</sup>, <sup>1</sup>St. George's Hospital, London; <sup>2</sup>INRA Station de Recherches Avicoles, Nouzilly, France.*

The archistriatum is a relatively large heterogeneous region of the caudal basolateral avian telencephalon and at least part of it is considered to be homologous with the mammalian amygdala. Previous research implicated the archistriatum in the tonic immobility fear responses of quail chicks but it was not known if this effect would also

be apparent in adults. Here, we assigned Japanese quail chicks of a line selected for long tonic immobility reactions to one of three treatment groups bilateral electrolytic lesions of the archistriatum (ARCH), bilateral electrolytic lesions of the lateral cerebral area (LCA) and unoperated controls (U). Lesions were made when chicks were 3-5 days old. At 12 weeks of age, ARCH quail showed significantly less avoidance of a novel object and pecked sooner at novel food. They also showed numerically less avoidance of a human being than did LCA or U birds. These results demonstrate that the archistriatum is involved in a variety of behavioural fear responses and that the effects of archistriatal lesions in young chicks persist into adulthood.

THE FACE INFERIORITY EFFECT IN PIGEONS. *Francisco J. Donis, Department of Psychology, Central Connecticut State University, U.S.A.*

The "face superiority effect" is a well-known phenomenon. This effect is demonstrated, in humans, when target facial features are recognized faster if they are presented embedded in a human facial context than in isolation. One possible explanation for this effect is that, for humans, whole facial forms but not isolated features have ecological value. With pigeons, on the other hand, it is predicted that in similar situations the addition of human facial contexts will be detrimental to the discrimination of target facial features. This hypothesis was investigated in two experiments in which a successive discrimination task was used. In Experiment 1, there were 4 pigeons in each of three conditions. Pigeons in Condition 1 were required to discriminate between two U-shapes, one in the upright position and one in the inverted. Three dots in a triangular formation were added to each of the two U-shapes in Condition 2, and the U-shapes plus the 3 dots were embedded in a facial context in Condition 3. In Experiment 2, 5 pigeons were required to make the three discriminations of Experiment 1. The results came out as predicted. That is, instead of a "face superiority effect," a "face inferiority effect" was obtained in the two experiments.

A COMPARATIVE APPROACH TO RECONCILIATION. *Paula Maria de Almeida Fríoli and César Ades, Institute of Psychology, University of São Paulo, Brazil.*

In a wide variety of non-human primate species, soon after a fight, opponents tend to approach one another, and display a relatively high level of affiliative behaviour. De Waal and van Roosmalen (1979)

first interpreted such behaviour as a form of repairing a damaged relationship, and used the name *reconciliation* to label it. Reconciliatory behaviour seem to reduce the probability of further conflict and to restore tolerance between former opponents. But has reconciliation thus defined any similarity to human reconciliation ? Using as a starting point published reports on nonhuman primate reconciliation, we videotaped spontaneously occurring conflicts among preschool children (4 to 7 years old) during free activity in a school yard. Threats, verbal and overt aggressions, submissive, affiliative and reconciliatory behaviours, were among the chief behavioural categories used for analysis. Results indicated age and gender differences, some of them in expected directions (boys' higher rate of threats and overt aggressive acts, for instance), more reconciliation between same gender, and between friends; and some new, such as the higher rate of reconciliations initiated by girls. The results indicate that reconciliation in human seem to have the same function that in nonhuman primates (maintain social behaviour that benefits involved individuals).

CATEGORICAL USE OF SIGN LANGUAGE BY CROSS-FOSTERED CHIMPANZEES. *R. Allen Gardner, Department of Psychology, University of Nevada, Reno, U.S.A.*

Vocabulary tests show that the signs in the vocabularies of cross-fostered chimpanzees named natural language categories, DOG for any dog, FLOWER for any flower and so on. Errors on these tests showed that these categories form groups such as animates, edibles, and household objects. Answers to systematic samples of WH-questions such as WHAT THAT?, WHAT COLOR THAT? and WHO THAT?, show further organization into functional categories that parallel findings in similar studies of human children.

COMPARATIVE INTELLIGENCE AND INTELLIGENT COMPARISON. *R. Allen Gardner, Department of Psychology, University of Nevada, Reno, U.S.A.*

Intelligent tasks administered under stimulating conditions reveal significant overlap in the intelligent behaviour of human and nonhuman animals. Mind-numbing drill masks the intelligence of human and nonhuman animals.

INTEGRATIVE LEVELS, THE BRAIN, AND THE EMERGENCE OF LANGUAGE AND CULTURE. *Gary Greenberg, Department of Psychology, Wichita State University, U.S.A.*

Taking an epigenetic and anagenetic perspective, we present a theory of behavioural evolution by grades. The nervous system and behaviour increase in complexity with evolutionary advance. We link the emergence of complex social behaviour to brain evolution and the appearance of language. In making these links, we rely on applications of dynamic systems theory and show how the emerging sciences of complexity have much to offer behavioural science.

A BRIEF OVERVIEW OF THE EARLY PLIOCENE FAUNA IN SOUTH WESTERN CAPE. *Philippa Haarhoff, Earth Sciences Division, South African Museum, South Africa.*

This talk will focus on the fossil fauna from the site known as Langebaanweg. The site is situated about 110km northwest of Cape Town. Based on the research that has been done, it is evident that five million years ago the Cape west coast was inhabited by a diverse range of animals living under quite different climatic conditions than are presently experienced in this region. Some time will also be devoted to discussing how this site can possibly be used for further research, education and tourism programmes and how these programmes can raise awareness in environmental issues.

DEVELOPMENT OF DUSTBATHING BEHAVIOUR IN YOUNG CHICKS. *Jerry A. Hogan, Dept. of Psychology, University of Toronto, Canada and Klaus Vestergaard, Dept. of Animal Science, Royal Veterinary University, Copenhagen, Denmark.*

The sequential structure of dustbathing bouts was investigated in two studies. In the first, junglefowl chicks were observed on sand for 1 hr a day between 7 and 15 days posthatch. All dustbathing components were seen in bouts from day 8, and the temporal order of the components was similar to the order seen in adults. In the second, domestic chicks were observed on either sand or wire between 2 and 23 days posthatch. In even the youngest chicks (2-5 days) significant sub-bouts of dustbathing components were seen, and a more complex, adult-like structure was seen by 8 days. A Markov-chain analysis showed that both groups of chicks developed a basic rigid bout structure, but various aberrations also developed in the birds raised on wire. These results are compared with the development of grooming bouts in rats: in both species, the organization of the grooming elements

is independent of the development of the individual behaviour components.

AN ANALYSIS OF THE RESPONSE-TO-CHANGE PHENOMENON IN HOODED RATS. *Robert N. Hughes, Department of Psychology, University of Canterbury, New Zealand.*

Over 40 years ago Kivy, Earl and Walker (1956) demonstrated that, after having been allowed to see into but not enter the two white or black arms of a T-maze by means of transparent barriers, rats entered first the arm that had changed to opposite brightness. Immediately afterwards, Dember (1956) reported a similar preference for brightness change when the change was from a black and white arm to either two black or two white arms. Although Dember's experiment was designed to distinguish between two explanations for spontaneous alternation, it has more recently been used as a measure of short-term memory, attention or information processing. The present paper describes comparisons between the two change paradigms that involved measures of the first arm approached (as well as entered), and time spent in and entries of each arm during a three-minute period by hooded rats in either a Y- or a T-maze. The results were significantly affected by the type of apparatus, the brightness change paradigm, the sex of the rats and whether the change involved one from black to white (or vice versa) irrespective of the type of change. Implications for the study of intrinsic exploration and/or its underlying behavioural processes in different species will be discussed.

Dember, W.N. (1956). Response by the rat to environmental change. *Journal of Comparative and Physiological Psychology*, 49, 93-95.

Kivy, P.N., Earl, R.W. & Walker, E.L. (1956). Stimulus context and satiation. *Journal of Comparative and Physiological Psychology*, 49, 90-92.

LITERACY AND IDENTITY CONSCIOUSNESS: SOME PERSPECTIVES FROM THE NORTHERN CAPE. *Anthony J. B. Humphreys, Department of Anthropology and Sociology, University of the Western Cape, South Africa.*

A notable feature of present day South Africa is the aggressive reclaiming and assertion of indigenous identities. Many of these had hitherto been forgotten or denied in the face of colonial and apartheid oppression. A striking element in this process of identity reclamation is the implicit or explicit assumption that such identities are somehow 'primordial' in nature. These assumptions are evident in academic writing as well as in the claims made by the various identity groups themselves. This prevailing scenario presents particular challenges to

archaeology. To what extent can the archaeology of these asserted identities be traced back in time? In this presentation consideration will be given to the consequences of literacy for identity consciousness and the role that the written record plays as a resource in the assertion of the 'primordial' nature of indigenous identities. The area north of the Orange River will be used as a case study to generate models which might have wider relevance.

THE EVOLUTION AND DEVELOPMENT OF THE I.S.C.P. *Nancy K. Innis, Department of Psychology, University of Western Ontario, Canada.*

In the summer of 1983, a small group of comparative psychologists met at York University in Toronto, Canada to formally establish what is now the International Society for Comparative Psychology. The first meeting at which papers were presented and an executive elected took place the following year in Acapulco, Mexico in conjunction with the meeting of the International Congress of Psychology. In this paper, I will outline the development of our society from the early efforts of Ethel Tobach that resulted in the Toronto meeting to our current status as we meet in Cape Town, South Africa in 1998.

INTERACTIONS OF BEHAVIOURAL ELEMENTS IN THE SPOTTED DEER, *AXIS AXIS*. *T.V. Jayarani and M. Balakrishnan, Department of Zoology, University of Kerala, India.*

The behavioural activities, behavioural sequences and behavioural clusters of the spotted deer, *Axis axis* were studied in the Trivandrum Zoo. Altogether, 70 behavioural elements were noticed during a total of 454 hours of observations spread over 30 months. The duration, sequence and frequency of each activity during the unit observation period of two hours were computed. the frequency of transition of one element of activity to another was examined to find out behavioural dependence and their interactions. A chi-square test of independence was carried out to reveal differences in the transition of activities. Various behavioural interactions of 2-5 string combinations were revealed. There was a close relationship between the acts of resting, chewing, self grooming and self licking. A cluster of resting, self licking, stretching body parts, sniffing and chewing, sniffing and resting and rubbing by antlers was observed among males. Standing, self grooming, sniffing and roaming, roaming, sniffing and standing, rubbing with hooves, sniffing and eating, eating, pedal marking, self

grooming and self licking, following others and allo-sniffing formed another cluster among males. Among females, resting, self grooming, self licking, sniffing and chewing, chewing, stretching body parts, rubbing body parts on environmental objects, sniffing, sniffing and resting and sniffing and standing formed the behavioural elements of one cluster, whereas, sniffing and roaming, roaming, standing, self grooming and self licking, sniffing and eating, eating, rubbing with hooves, pedal marking (a behaviour by which artiodactyles purposefully stamp on the ground by their feet), allo-sniffing and biting were those of the other distinct cluster. Distinct clusters of elements of olfaction, feeding, aggression and social activities were revealed. Allo-grooming, allo-licking and allo-sniffing were prominent during heterosexual interactions. Behavioural interactions were influenced by sex, age, motivational states, physiological factors, duration of previous act and the number of individuals in the herd. There was sexual dimorphism in the association of behavioural acts, transition of behavioural elements and in the formation of behavioural clusters in the spotted deer.

**PECKING AT COLOURED STRING BY ADULT LAYING HENS: PREFERENCES AND STABILITY.** *R. Bryan Jones and Nina L. Carmichael, Division of Environment and Welfare, Roslin Institute, Scotland, U.K.*

Few studies have attempted to identify the influential features of devices intended to attract and sustain the interest of captive animals. We have already shown that young chicks peck more at string than at beads, baubles, chains or feathers. Here, we focussed on the effects of varying one specific feature of string, i.e. colour, on the pecking responses of individually-caged adult laying hens. In Experiment 1 we presented the birds with one of four differently coloured (white, yellow, orange or blue) bunches of string on four consecutive days, using a fully balanced Latin square design. This procedure was repeated after 6 weeks. White and yellow bunches of string were pecked much sooner and more often than the orange or blue ones in both trials. Though 9 of the 21 birds shifted preference across trials, none switched to orange or blue. In Experiment 2, previously untested hens were presented simultaneously with white and blue strings (the most and least attractive, respectively) at 80 and 86 weeks of age. White string again attracted considerably more pecking than did blue in both trials. We concluded that hens pecked readily at bunches of string, that white or yellow were the most attractive colours, that preferences were largely



stable, and that, encouragingly, pecking increased rather than habituated with repeated exposure. Establishing the birds' preferences for pecking stimuli and their component features will guide the development of environmental enrichment stimuli and/or devices intended to divert potentially injurious pecking away from other birds.

**SOCIAL DISCRIMINATION IN GENETIC LINES OF QUAIL SELECTED FOR CONTRASTING SOCIAL MOTIVATION : AN OVERVIEW.** *R. Bryan Jones, Division of Environment and Welfare, Roslin Institute, Scotland , U.K. and Andrew D. Mills, Station de Recherches Avicoles, France.*

Genetic lines of Japanese quail that have been divergently selected for low (LSR) or high (HSR) levels of social reinstatement (SR) behaviour on a treadmill show corresponding differences in underlying social motivation. HSR quail also show persistent agitation when isolated whereas LSR ones are virtually unaffected. Such selection may have important implications for welfare and performance but we must determine if other important characteristics or capabilities have been unconsciously influenced. Here, we report the results of three experiments focussing on social discrimination. Firstly, we showed that SR behaviour was species-specific, chicks of both lines ran on a treadmill to maintain contact with other Japanese quail but not with groups of domestic chicks, guinea fowl or an empty goal box. Secondly, when reared in groups of three, both LSR and HSR chicks discriminated between familiar cagemates and strangers of the same genetic line in a two-choice runway test. Thirdly, whereas HSR quail preferentially approached and stayed near chicks of their own line rather than LSR ones regardless of whether the stimulus birds were presented singly or in small groups, LSR quail showed no such social preferences. Collectively, these findings suggest that selection for high social motivation has not affected social discrimination in HSR quail. Conversely, though they recognized their own species as well as familiar individuals of their own line, line discrimination was compromised in LSR birds. We do not yet know if the latter result reflected a simple lack of this social preference, impaired discrimination or increased attention to the novel test environment.

TONIC IMMOBILITY FEAR REACTIONS IN AGED QUAIL GENETICALLY SELECTED FOR CONTRASTING ADRENOCORTICAL RESPONSIVENESS. *R. Bryan Jones, Division of Environment and Welfare, Roslin Institute, Scotland, U.K., and Daniel G. Satterlee, Louisiana State University, U.S.A.*

Divergent lines of Japanese quail have been genetically selected over several generations for a low (LS) or high (HS) plasma corticosterone response to brief immobilization stress. Selection of the LS line has been accompanied by reductions in general fearfulness (predisposition to be easily frightened by a variety of alarming events) and in physiological responsiveness to diverse stressors. These findings have important strategic implications because intense or prolonged fear and distress can seriously harm poultry welfare and productivity. However, these comparisons were all carried out in juvenile quail and, because the same characteristic may be affected by different genes throughout ontogeny as well as by environmental variation, it was important to determine if line differences in fear were still evident in mature birds. Therefore, we measured tonic immobility (TI) fear reactions to brief manual restraint in male and female quail of the LS and HS lines at 18 weeks of age. Our finding that males and females showed similar TI responses suggests that there are no sex differences in underlying fearfulness. Quail of the HS line showed considerably longer TI responses and, hence, greater fearfulness than the LS birds. This finding parallels our earlier findings in juvenile quail and demonstrates that line divergence in this characteristic does not disappear with increasing age. Our studies may identify simple, non-invasive behavioural tests that could be used as selection criteria for future breeding programmes intended to reduce fear and distress.

EFFECTS OF MATURATION AND HABITAT LOCATION ON RESPONSIVENESS TO HUMAN-EVOKED STIMULI IN COLOBUS MONKEYS. *Olufemi Adigun Lawal and Taiwo Omotunde Animashaun, Department of Psychology, University of Lagos, Nigeria.*

Naturalistic observations with intervention were carried out on two different populations of Colobus Monkeys [*Colobus abyssinicus*] which were found in two different habitats. The two habitats were operationally defined as "more natural" and "less natural" because they were of minimum and maximum human interferences, respectively, due to their locations in the environment. This observation was aimed at studying the extent to which the monkeys' responsiveness-habituation and sensitization, to certain human-evoked stimuli (stimuli evoked

through human interference), could be affected by their stages of maturation (growth), and location of their habitat in the environments. The results showed that the younger monkeys in both habitats demonstrated a significantly higher habituation and less sensitization than the older or adult monkeys. Habituation appeared to decrease while sensitization increased with increase in maturation of the monkeys. It was also found that the monkeys of the more natural habitat showed less habituation and more sensitization than the monkeys of the less natural habitat regardless of the limiting effects of the stages of maturation. It was concluded that the more natural a habitat is, the more likely adaptive it would be for preserving animal instincts; therefore, the less likely it may be for its animal subjects to benefit from learning.

DECREMENT OF DOMINANT RAT AGGRESSION LEVEL INDUCED BY AN UNPREDICTABLE STIMULUS. *Andres P. Lemoine, Lorena Rela and Enrique T. Segura, Faculty of Psychology, University of Buenos Aires and Institute of Experimental Biology and Medicine, Argentina.*

Learned helplessness (LH), a syndrome originally attributed to the lack of control, was found to be elicited by unpredictable stimuli (Overmeier & Seligman, 1967; Lemoine *et al*, 1994). It has been previously shown that both individual behaviour, central noradrenergic neurotransmission and adrenocortical catecholaminergic secretion are modified by uncontrollable and unpredictable stressors, but remained within the basal range when the animals received the same amount of uncontrollable but predictable stimuli. The behavioural literature showed that predictability, through relief and relaxation elicited by safety cues (in our case, constant ITIs) can reduce the aversiveness of inescapable shocks. On the other hand, unpredictable stimuli (in this case, variable ITIs) result in a state of chronic fear, which accounts for the observed behavioural impairment. According to Williams (1987), this occurs through the displacement of several behaviours, such as freezing (the stress-coping-fear-defense hypothesis). Due to the potential relevance of LH in the study of human depression (Gray, 1987), we decided to investigate the possible effects of these two treatments on the social status of randomly formed pairs of experimental animals. Again, a transient change in the hierarchical status of dominants rats was observed. This poster focuses on further evidence concerning the phenomenon of transient dominance reversion in rats, assessing aggression between the dominant and submissive

subjects of each dyad. Pairs of naive Sprague-Dawley rats (adult males) were randomly formed 1 month before testing. Dominance was assessed pre- and post-treatment of dominant animals with variable or constant ITIs. Dominance was assessed by scoring priority to access to a time-limited water source, displacement from the source, time in contact with the source (available for 10 s every minute during the 30 min. test), agonistic behaviours (boxing, stepping, etc) and individual behaviour as indicators of distress (such as autogrooming). The amount of time spent near the limited source of water was also measured. Accessory data are also shown, such as context preference and behavioural impairment in a simple task acquisition. The reported data supports our previous observations, showing that unpredictable treatment of dominants with inescapable shocks leads to a transient but significant reduction of its social status, due mainly to a reduction of its aggressive display.

SEEING AND BELIEVING: NATURAL BEHAVIOUR AND THE PROBLEM OF CAUSATION. *William A. Mason, Department of Psychology, University of California-Davis, California, U.S.A.*

Descriptions of the spontaneous behaviour of animals in natural settings is an essential part of scientifically understanding them. These accounts characteristically focus on biologically important activities, such as finding food, mating, avoiding predators and caring for young. Individual behaviour is usually described in everyday language that presumes the animal being observed is capable of perceptions, intentions, decisions, emotions, memories, and the like. Thus, an individual may be described as attending to an unusual sound, hesitating before deciding to cross a stream, and threatening, fearing, or affiliating with another member of its group. These terms are required to render a coherent and intelligible account of what an animal is doing as it goes about its normal routine. In addition, however, observers often believe that the terms they are using descriptively refer to psychological processes and states that are the causes of an animals behaviour and thus explain its actions. This belief confounds the fundamental distinction, traditional to comparative psychology, between the perceived functions of behaviour (an animals achievements) with its immediate causes (the factors that make the achievements possible). The relevance of this distinction to will be illustrated by contrasting descriptive accounts with experimental analyses of identical functionally defined behaviour categories in the same species.

**DIRECT ENVIRONMENTAL CONTROL OF MYOPIA.** *Sally A McFadden, Department of Psychology, University of Newcastle, Australia.*

Comparative studies with animals have led to new insights into the causes of myopia (short-sightedness). In particular, it has been clearly shown that direct manipulation of the visual input to the eye (by placing occluders or spectacle lenses over the eye) early during development can cause significant disruption to normal eye development and result in large refractive errors. Such studies implicate a visual control mechanism which guides normal eye development. However, the precise stimulus which drives eye growth is unclear, but has been variously proposed to include form (spatial frequency), blur, chromatic aberration, accommodation, brightness, image magnification and temporal modulation. Defining the stimulus is important, as it has consequences for knowing how one might reverse abnormal refractive errors and myopia development in children. We set out to see if changes in the visual environment alone, without lenses or occluders, could control eye growth in a popular animal model of experimentally induced myopia. In particular, we tested whether we could induce changes in normal eye growth in chicks by directly modifying the spatial frequency and contrast of their visual environment. Groups of 10 white leghorn chicks were individually raised from day 1-10 in cylindrical arenas which were completely wall-papered with specific visual stimuli made of black and white gratings (subtending between 1-4 cycles/degree) evenly illuminated on a 12/12hr light/dark cycle. Six levels of contrast were used between 0 (no contrast) and 1 (high contrast) with the mean level of brightness and illumination equal in each group. At the end of the raising period, optical measures were taken of the eye including refractive error (measured with streak retinoscopy under ketamine/rompun anaesthesia), corneal curvature, choroid thickness and axial and equatorial length measurements. When raised in cubicles without wallpaper, chicks were +5D hyperopic on day 1 and emmetropized to +0.5D by day 14. However, when raised with the wallpaper, both axial length and refractive error were found to be linearly dependent upon contrast level, with the lowest levels of contrast producing the most myopic eyes (mean 3.5D) with the greatest axial length and higher contrast levels resulting in successively less myopia. The lowest contrast wallpaper produced up to 6D of myopia in individual chicks. Thus we find that eye growth and the development of myopia in the chick can be produced without occluders or lenses and depends directly

upon the degree of contrast in the visual environment. These results have implications for the role of near-work in inducing myopia, and possible implications for the reversal of myopia in young children.

#### LOCALIZATION OF OBJECTS IN 3D SPACE: THE AVIAN WAY.

*Sally A McFadden, Department of Psychology, University of Newcastle, Australia.*

Birds have highly evolved visual systems. In negotiating a three dimensional world, they have evolved elegant strategies, the optical and neural mechanisms of which are partially set through early behavioural experience. Their solutions to decoding three-dimensional space provide a fascinating insight into the rich diversity of biological solutions for decoding the physical world and the intimate interaction between these biological solutions and their behavioural impact. This paper will examine these issues from an avian perspective and comment on the unique contributions of the comparative psychological approach.

#### EASE OF CAPTURE IN LINES OF JAPANESE QUAIL GENETICALLY SELECTED FOR CONTRASTING FEARFULNESS OR SOCIALITY.

*Andrew D. Mills and Jean M. Faure, INRA Station de Recherches Avicoles, Nouzilly, France.*

Although human-animal interactions are of fundamental and strategic importance, the role of genetic factors in reducing animals' fear of humans has received comparatively little attention. The present study examined the effects of genetic selection for contrasting fearfulness or sociality on the ease of capture of Japanese quail. We used quail of the F16 generations of lines selected for long (LTI) or short (STI) tonic immobility (TI) fear reactions (a measure of underlying fearfulness) or for high (HSR) or low (LSR) levels of social reinstatement behaviour on a treadmill (a measure of sociality). Two mixed-line groups were reared in floor pens from hatching. One comprised 241 LTI and 250 STI quail whereas the other was composed of 178 HSR and 168 LSR birds (differential mortality caused uneven numbers within groups). Constraints dictated the use of this design which effectively allowed no replicates. At 2, 4 and 6 weeks of age all birds were caught individually and their identity and capture rank were noted. At all ages, STI and HSR quail were caught significantly sooner than LTI and LSR ones. Capture ranks measured at each age were significantly correlated and there were no significant effects of age either between or within lines. Though the present findings contrast with those of selection programmes carried out elsewhere, we propose

that selection for reduced tonic immobility or for enhanced sociality produced quail that are less fearful of humans and thereby easier to capture.

#### STRESS RESPONSES IN LINES OF JAPANESE QUAIL SELECTED FOR LONG OR SHORT TONIC IMMOBILITY FEAR REACTIONS.

*Andrew D. Mills, Herve Remignon, Daniel Guemene and Jean M. Faure, INRA Station de Recherches Avicoles, Nouzilly, France.*

The importance of comparative psychology in improving animal welfare is widely recognised but its potential contribution to production has often been ignored. Here, we asked whether stress-induced reductions in meat quality would differ between Japanese quail of two lines divergently selected for long (LTI) or short (STI) tonic immobility fear reactions. In Experiment 1, LTI and STI birds were subjected to physical restraint in a crush cage for 15 min immediately before slaughter whereas quail were exposed to transportation stress and attendant food deprivation for 1 hour in Experiment 2. STI quail struggled more during restraint and showed greater increases in plasma corticosterone levels following exposure to either stressor than did LTI birds. However, measures of meat quality (pH and water loss) taken immediately after slaughter and 24 h postmortem were significantly better in STI than LTI quail. These findings support the growing contention that the reduction of fearfulness has greater relevance to animal production than has been previously recognised.

#### AVERSION IN THE ELEVATED PLUS-MAZE. I. ROLE OF VIBRISSAE. *Silvio Morato and Fernando Cárdenas, Institute of Psychology, University of Sao Paulo, Brazil.*

Thigmotaxis, or the tendency to keep the vibrissae in contact with vertical surfaces, is considered to be an important determinant of rat exploratory behaviour in the elevated plus-maze. In order to evaluate the role of vibrissae stimulation in that experimental model of anxiety, 96 rats had either part (tip or half) or whole vibrissae removed, or kept intact in control animals. Immediately after removal, half of the rats were submitted to an elevated plus-maze for 5 min under normal light (a 60-W white bulb) while the other half were tested in the dark (a 20-W red bulb). The bulbs were placed 1.75 m above the centre of the maze. The time spent in the open arms under normal light was decreased after removal of the tip, half, but not of the whole vibrissae, when compared with control rats with intact vibrissae. There were no significant differences when the animals were tested in the dark, but in

this condition all groups spent significantly more time in the open arms than the rats tested in normal light. The fact that under light condition, but not in the dark, partial removal of vibrissae caused anxiogenic effects suggests that other sensory modality, like vision, may be mediating aversion to the open arms.

**AVERSION IN THE ELEVATED PLUS-MAZE. II. ROLE OF VISION.** *Silvio Morato and Juan Carlos Martinez, Institute of Psychology, University of Sao Paulo, Brazil.*

The elevated plus-maze test is usually run with a 1-cm edge surrounding the open arms in order to prevent the rats from falling. The initial objective was to investigate the role of transparent edges differing in heights: 1, 5, 10, 20 and 40 cm, the latter the same height as the closed arm walls. This 40-cm high transparent edge was also studied covered by white translucent or black opaque paper. The data show that the time spent in the open arms was significantly greater when the edge height was 5, 10 or 40 cm covered by the white or black paper. However, there were no differences from the 1-cm control edge when the height was 20 or 40 cm transparent. A similar effect was observed when entries in the open arms and total entries were analysed. The facts that there were no differences when the open arms were surrounded by 1- or 40-cm transparent edges (which allow thigmotaxis) and that the same 40-cm edge caused increases in exploratory behaviour when covered by papers indicate that vision and touch are important determinants of aversion to the open arms. It is also possible that sensory modalities are hierarchically organized.

**EFFECT OF CAT URINE ODOUR ON RAT EXPLORATORY BEHAVIOUR IN THE ELEVATED PLUS-MAZE.** *Silvio Morato and Marisol Lamprea, Institute of Psychology, University of Sao Paulo, Brazil.*

The elevated plus-maze is an animal anxiety test based on the natural tendency of rodents to explore novel environments and at the same time to avoid unsafe places. It consists of two open arms opposed to two closed arms, i.e., surrounded by walls. A rat will typically explore the closed arms more than the open ones. The present experiment investigated the effect of cat urine smell placed either in the open or the closed arms. The cat urine was placed under the floor of the maze and the rats could smell it through holes but otherwise had no access to it. The results indicated that the rats entered the open arms more often when cat urine was placed in them than when it was not



present or placed in the closed arms; no differences were observed in the entries into the closed arms. They also spent more time in the open arms when cat urine was placed there than when it was not present or placed in the closed arms but the difference was statistically significant. These results suggest that the smell of a predator caused the rats to explore more the usually avoided places.

**PERSISTENCE OF APPARENTLY SUPERFLUOUS AND DELETERIOUS BEHAVIOUR ACROSS GENERATIONS.** *Robert M. Murphey, Department of Psychology, University of California - Davis, U.S.A.*

Excepting its lack of purpose, natural selection is analogous to mass screening in behaviour genetic experiments, as described by Hirsch and Tryon (1956). They showed that successful selection is not possible when variation within and among individuals becomes equal. Stated differently, selection cannot take place when test-retest reliabilities of observation procedures are inadequate for discriminating among individuals. Considering the reliability of natural selection as variable and sometimes low, the persistence of apparently superfluous and deleterious behaviour across generations can be accounted for without recourse to contrived causal explanations such as undiscovered pleiotropic effects, balanced polymorphisms, gene linkages, hidden adaptive value of characteristics that are ostensibly non-advantageous, and the perseverance of selectively neutral traits that once had reproductive utility. Perhaps paradoxically, effective natural selection diminishes its own reliability.

Hirsch, J. & Tryon, R.C. (1956). Mass screening and reliable individual measurement in the experimental behaviour genetics of lower organisms. *Psychol. Bul.*, 53, 402-410.

**INSTRUMENTAL LEARNING IN TOADS (*BUFO ARENARUM*) AND AVERSIVE REINFORCEMENT.** *Rubén N. Muzio, Mariano A. Loza Coll and Lorena Pompilio, Institute of Experimental Biology and Medicine, Argentina and University of Buenos Aires, Argentina.*

During the last decade we have been studying several learning phenomena in toads (*Bufo arenarum*) with a training situation in which water was an appetitive reinforcer. Using this sort of reinforcer it has been possible to observe acquisition and extinction (under massed and spaced training conditions), spontaneous recovery, the reward-following effect, and the magnitude of reinforcement acquisition effect. At present we are interested in beginning the study of aversive learning in amphibians. Most of the experiments concerning aversion in

vertebrates use an electric shock as aversive stimulus, while a few others use bright lights or noises. However, these stimuli seem not to be as effective in amphibians as in other groups. In order to find an adequate aversive stimulus for toads, and taking into account the experiments previously developed in our laboratory concerning the electrolyte sensitivity of the skin in this species, we began to study the behaviour of toads in contact with NaCl solutions of several concentrations. Theoretically, according to the concentration of these solutions, we could obtain an aversive stimulus (a highly concentrated solution), in which the animals lose weight. In addition, it would be also possible to find a "neutral stimulus", this is a solution in which the animals show no effect on water uptake (neither win nor lose weight). These issues were studied in a spaced-trial experiment in which 3 groups of toads received 15 R trials with deionized water during acquisition. Then, each group was changed for 13 trials to one of the three following conditions: a 1M NaCl solution (Group R-1M), a 0.3 M NaCl solution (Group R-0.3M), or to extinction -with N trials- (Group R-N). In acquisition, terminal performance was similar among all the groups. Subsequently, Group R-0.3M showed lower latencies than the other two from the third post-shift session. Group R-1M showed a rapid increase of the latencies after the shift and differed from Group R-N at the terminal level. The water uptake of the Group R-1M showed negative values during the post-shift phase. In contrast, the water uptake of the Group R-0.3M began to increase from the third post-shift session, what correlates with the performance of the group, which decreased from the same session. This fact might be seen as an adaptative adjusting to the new external conditions. Finally, highly concentrated NaCl solutions having shown to be an efficient type of aversive stimuli for the toads and may be used in the future as a new kind of stimulus in the study of several learning phenomena in this group.

ANIMAL INTELLIGENCE ESTIMATED BY AMERICAN AND JAPANESE UNIVERSITY STUDENTS. *Sadahiko Nakajima and Kohki Arimitsu, Department of Psychology, Kwansei Gakuin University, Japan and K. Matthew Lattal, Department of Psychology, University of Pennsylvania, U.S.A.*

University students from the US and Japan rated the intelligence of each of 54 kinds of animals (e.g., chimpanzee, whale, dolphin, dog, cat, horse, rat, bat, parrot, pigeon, owl, frog, snake, ant, honeybee, earthworm, amoeba) relative to that of humans, which was assigned 100 points. Differences and similarities in the ratings in these

two populations were examined. In addition, cluster analyses were conducted to reveal the underlying structures of their belief systems. Implications for animal right movements, whaling, wildlife, anthropomorphism, and cross-cultural understanding of these animal-related issues are discussed.

**INTEGRATIVE LEVELS IN COMPARATIVE PSYCHOLOGY - THE EXAMPLE OF EXPLORATORY BEHAVIOUR** *Wojciech Pisula, Department of Psychology, University of Warsaw, Poland.*

Comparative psychology is a discipline with no clear paradigm. The majority of researchers who examine problems of animal behaviour refer to Tinbergen's four questions about behaviour or to the proximate / ultimate causation dichotomy. This paper includes discussion of the approaches adopted by Tinbergen, Mayr and Dewsbury, as well as the proposal of structuralization. The theory of integrative levels provides an alternative to the reductionist approach to understanding behaviour. The potential value of using an approach based on the integrative levels theory is described here using exploratory behaviour as an example. This strategy addresses fundamental questions about animal behaviour as well as the potential problem of individual differences.

**TRANSITION AND STEADY STATE PROBABILITIES OF BEHAVIOUR OF THE SPOTTED DEER, AXIS AXIS.** *R. Reshmy and M. Balakrishnan, Department of Zoology, University of Kerala, India.*

Transition and steady state probabilities of behaviour of the spotted deer, *Axis axis* was studied in Trivandrum Zoo by observing 59 behavioural elements belonging to eight major behavioural states such as the acts in relation to: 1. antagonism, 2. sniffing, 3. licking and grooming, 4. reproduction, 5. scent marking, 6. eating, 7. parental behaviour and 8. general behaviour. The spotted deer spent most of their time in acts related to eating, general behaviour and licking and grooming. The transition probability was greater for behavioural states concerned with general behaviour and licking and grooming. The probability of the animal of either sex and age group to be in acts in relation to general behaviour and licking and grooming after any one of the eight states was more when compared to other behavioural states. The probability to be in antagonistic behaviour was comparatively less for females. Acts in relation to scent marking were more evident in the case of male behaviour. Parental behaviour was not seen among males. The stationary probability distribution for states of antagonism and

scent marking was higher among males. The influence of each of the major states of behaviour to elicit or inhibit certain acts also vary with sex.

ENVIRONMENTAL INFLUENCE ON HOMINID DEVELOPMENT IN SOUTH WESTERN CAPE. *Dave Roberts, Council for Geoscience, South Africa.*

Consensus is emerging that the chimpanzee-hominid split occurred at ~5Ma. Currently the most primitive and oldest hominid known is the Ethiopian *Ardepithecus ramidus*. There is no evidence for hominids of such antiquity anywhere in southern Africa. Rather than constituting evidence that earliest man was confined to tropical east Africa, this may be a manifestation of the dearth of geological strata of this age. In the southwestern Cape, the Varswater Formation has yielded fossils from this critical period, including spectacular carnivores such as giant bears, wolverines and sabre-tooth cats. Generally, the fauna and flora reflect a warm, humid climate, with both woodlands and grasslands, suitable for hominid habitation. Recently, a hominoid tooth was found in Miocene strata further north in Namaqualand, suggesting that we should look more closely at the Varswater deposits. Drift of continental land-masses in circum-polar regions resulted in cold currents along the west coast in post -Varswater times; consequent cooling and drying of the climate ushered a dramatic change in the vegetation to the sclerophytic "fynbos". Pliocene australopithecines have been unearthed from localities as little as 800km northwestwards, but there is no evidence of human presence in the southwestern Cape until ~1.2 Ma; probably, the capacity to adapt to the harsher local conditions came after these times; alternatively, geographic barriers like the Cape Fold Belt inhibited migration into the region. In the Pleistocene, the climate alternated from cold glacial to (brief) interglacials driven by wobbles in the Earth's orbit around the sun. Large, early Acheulian hand-axes associated with moist, protected riverine valleys are the earliest testimony to the presence of man; evidence from elsewhere suggests that habitation was restricted to the warmer times. At Hopefield, the skull-cap of Saldanha Man (early Archaic *Homo sapiens*) dated to ~ 500 ka is the oldest skeletal human remnant in the region. The climate was interglacial; hippopotami, semi-aquatic animals, were common. The Middle Stone Age (MSA) dating from ~250- 30 ka, presents the first evidence of widespread uninterrupted habitation throughout the climatic cycles; technological advances reflected in a diverse stone tool-kit provided the

necessary versatility. Much of the evidence lies beneath the sea, accumulating when sea levels were lower than today. Fossil human footprints found at Langebaan, dating from 117ka, dramatically record the passage of an early anatomically modern human along the pristine shores of a lagoon, at the end of the last interglacial. Twin threats from human interference and natural erosion prompted their recent removal to the National Museum, Cape Town. At ~20 ka, there was an extreme refrigeration, sea levels plunging by 130m, and temperatures by 5°C. The Holocene (the interglacial of the last 10ka) was marked by the extinction of several large herbivore species, unable to adapt to the rapid warming and sea level rise. Because people were living along the present shoreline, there is an abundance of artefacts from this era.

**A LONG VIEW OF HUMAN HISTORY IN SOUTH AFRICA: THE LAST 50,000 YEARS.** *Judith Sealy, Department of Archaeology, University of Cape Town, South Africa.*

This talk aims to sketch, in broad outline, the history of human occupation of southern Africa over the last 50 000 or so years. For all of this time, the inhabitants of southern Africa have been 'anatomically modern' humans, people physically indistinguishable from populations in the world today. This situation contrasts with that of Europe and western Asia, where non-modern Neanderthal populations continued to exist until about 30 000 years ago. African populations of modern humans may well have been ancestral to all humans in the world today; thus the history of these communities is of wide interest. Excavation of archaeological sites and examination of artefacts, food residues and other items enables archaeologists to reconstruct aspects of the lifeways of these long-dead societies. I will trace the development of technology and behaviour during the last 50 000 years, looking at issues such as the first evidence for art, the development of hunting techniques, including the adoption of the bow and arrow, and how these advances may have related to the social organisation of the time. All southern African people continued to live by hunting and gathering until only 2000 years ago, when sheep and perhaps cattle-keeping were introduced into the western and southern parts of the country, and the first mixed farmers, who grew crops and kept domesticated animals, settled in the northern and eastern areas. I will explore the reasons why farming should have been such a recent innovation in this region, and look at some of the consequences for southern African society today.

ADAPTIVE STRATEGIES OF KHOEKHOEN AND SOAQUA OF THE WESTERN CAPE. *Andrew B. Smith, Dept. of Archaeology, University of Cape Town, South Africa.*

When domestic sheep first appeared in the Cape c.1900 years ago the land was already occupied by hunting people who used marine and terrestrial resources. This paper will discuss the impact of pastoralism on aboriginal hunting society, and the adaptive strategies of herders which developed over time, as the herd composition changed from sheep to cattle. We can demonstrate archaeologically that two distinct economic groups continued to coexist in the landscape until historic times when the records of the Dutch settlement at Table Bay after 1652 describe contact with the Khoekhoen (pastoralists) and Soaqua (hunters). Within 60 years of colonial settlement aboriginal society around the Cape Peninsula had virtually disappeared, with the Khoekhoen either moving away, or becoming incorporated into Dutch farming society as lower class menials. Khoekhoen knowledge of the resources of the Cape was transferred to Dutch stock farmers, allowing them to expand into the interior, and to further disrupt aboriginal society.

PAINTINGS AND "BIG PICTURES": SAN ROCK ART IN GLOBAL PERSPECTIVE. *Anne Solomon, Department of Archaeology, University of Cape Town, South Africa.*

San rock art is of global interest for various reasons. On the one hand, questions of the production of art are linked to the emergence of "symbolic behaviour" and to the emergence of anatomically modern humans. On the other, South African research into San art has been used as the basis for understanding the origins of art, in European Palaeolithic sites such as Lascaux. In this paper I consider the shamanistic model, developed by Lewis-Williams (e.g. 1981) and his colleagues, which relates the production of visual art to altered states of consciousness and "neuropsychology"; and a model of the emergence of modern humans which relies heavily on Khoisan art and narrative (e.g Knight 1991; Power and Watts 1997). There is a productive tension in current research between such models, which emphasize global patterns, universals and the like, and those which insist on historical specificity. In considering this problem, questions of theory and method are highlighted, and some implications for our understanding of past visual production and "cognition" are outlined.

**A NEURO-EVOLUTIONARY APPROACH TO THE ANXIETY DISORDERS.** *Dan J. Stein and Colin Bower, Department of Psychiatry, University of Stellenbosch, South Africa.*

Advances in our understanding of the anxiety disorders and in the application of evolutionary principles to medicine provide the possible basis for a neuro-evolutionary approach to these conditions. In this paper, initial steps taken towards such an approach are described. Neuro-evolutionary accounts of each of the anxiety disorders have been offered. Notably, several of these accounts have suggested that particular anxiety disorders are mediated by specific brain-based false alarms. This paper reviews the strengths and weaknesses of such accounts. The false suffocation alarm of panic attack is the most fully elaborated of the neuro-evolutionary accounts of an anxiety disorder. However, viable neuro-evolutionary approaches have also been offered for other anxiety disorders such as obsessive-compulsive disorder and social phobia. Further work is necessary to consolidate a neuro-evolutionary approach to the anxiety disorders. Although the theoretical basis for such an approach has become increasingly appealing over the last several years, this foundation requires supplementation by further empirical research.

**BIODIVERSITY, GENOMICS AND COMPARATIVE PSYCHOLOGY.** *Ethel Tobach, Department of Mammology, American Museum of Natural History, U.S.A.*

Contemporary research in comparative psychology should be examined in the light of advances in the technology of genetic research and the changes in the relations between humans and their environment, an aspect of biodiversity theory. The apparent tension between the apparent needs of humans for survival and the changes in the global environment requires us to ask how comparative psychologists intent on understanding evolutionary and developmental processes in behaviour can contribute to formulating questions and answers that will attenuate the tension constructively. Biodiversity concepts and programs need to be analyzed as to whether they address the needs of people, and base their conclusions on knowledge about behaviour. The same examination is required of genomic programs as they involve all species, including humans. Suggestions are offered as to how the Society and the Journal can contribute to appropriate formulations of existing and nascent problems and their solutions.

STANDARDIZATION OF THE OPEN FIELD TEST - CONTINUED ASSESSMENT. *Maciej Trojan, Department of Psychology, University of Warsaw, Poland.*

The open field test is one of the most commonly applied procedures in animal behaviour laboratories. Paradoxically, the popularity of this test remains high despite the equally pronounced criticisms concerning the reliability, accuracy and interpretation of open-field results. My objective is to thoroughly assess the influence of selected features of the procedure and apparatus upon the behaviour of the experimental animals, laboratory rats in this case. This may, in turn, lead to recommendations concerning standardization of the open field. The results of some of our recent examinations of variables as diverse as: the colour and pattern of the floor and walls, ambient light intensity, handling, the presence or absence of the experimenter, the animals' age, and the presence and position of the start box are presented.

COMPARING DOLPHIN NEOCORTEX AND ITS EVOLUTION TO HUMANS AND OTHER PRIMATES: MACHIAVELLIAN INTELLIGENTSIA OR FORAGING PHILOSOPHERS? *Alain J-P. Tschudin, School of Psychology, University of Natal - Pietermaritzburg, South Africa.*

What drives and constrains the evolution of the brain, the cerebral cortex and intellectual capacity across different species and orders of mammals? Research has established that in primates, the relative size of the brain and its neocortex are more closely associated with the pressures of a social existence than to foraging or ecological demands. This does not appear to be the case for other terrestrial mammalian orders, whose neocortical evolution appears more closely related to foraging pressures than to sociality. The current study represents the first effort to establish interspecific dolphin neocortex ratios and examines these in relation to sociality and foraging ecology. Relative brain size has been established by using MRI, CT and/or Cranial Volume Analysis for 163 animals, comprising 19 different species of toothed whales and one primate species, humans. Dolphins have had to adapt to life in a highly complex environment, radically different to life on land. Local dolphin species exhibit a diverse range of social structure and foraging concerns, making them well suited to such a study. The preliminary findings of large neocortex ratios in dolphins, together with their relatedness to several social and feeding variables are of interest; while comparative analysis with human neocortical data is also of significance.



**FUNCTIONAL CATEGORIZATION OF OBJECTS IN ANUBIS BABOONS.** *Jacques Vauclair and Dalila Bovet, Centre de Recherche en Neurosciences Cognitives (CNRS), Marseille, France.*

Baboons were trained and tested on the natural category of food versus non-food with real objects using an adapted version of a WGTA. Subjects were first trained to categorize two objects, one food and one non-food; then, 80 other objects (40 food and 40 non-food) were presented and categorical response to each object was recorded. The baboons showed a good and rapid transfer of their categorical abilities to the novel items. In a subsequent experiment, two subjects were trained with cut-out photos of one object in each of the previously learned category, and then tested with a subset of photos of the objects used in the first experiment. After training with one pair of pictures, categorical transfer was high in both baboons for cut-out photos. Results of other experiments (not reported here) with whole pictures and with additional control situations involving various modes of picture presentations further demonstrate the abilities of the baboons to relate real objects with their pictorial representations.

**THE SMALL-EARED BUSHBABY (*OTOLEMUR GARNETTII*) AS A LABORATORY ANIMAL.** *Jeannette P. Ward, Department of Psychology, University of Memphis, USA.*

Because prosimians constitute the historical foundations of the primate order, it is important to understand their behavioural capacities and limitations. However, the behaviour of these primitive primates has been much less studied than that of anthropoid primates. This is particularly true of African prosimians that are difficult to observe in wild habitats because of their nocturnality. The prosimian group contains species of great variability in structure and behaviour, including many specializations that have evolved over their long evolutionary development. By comparison, bushbabies are quite generalized in body structure and adaptable to a variety of living conditions and thus might be considered somewhat prototypical. In 1985, our laboratory received a gift of 13 small-eared or Garnett's bushbabies (*Otolemur garnettii*) composed of 4 pairs brought from the wild in 1981 and their progeny. From these a breeding colony was established that continues to the present. This species has thrived in captivity to date with life-spans exceeding 17 years and 138 live births. They have adapted exceedingly well to colony life with no characteristic health problems for the animals or their human caretakers. Since their arrival the bushbabies have been engaged continuously as the subjects

of noninvasive behavioural research, teaching us much about their kind and furnishing insights into primate behavioural evolution. An overview of these studies and their conclusions will be presented, including 1) behavioural laterality, 2) visuo-spatial learning, 3) acquisition of fishing behaviour, 4) temperament and its relation to learning, 5) male birth sex ratio bias, 6) olfactory communication, and 7) current studies of social behaviour and vocalization. The purpose of this presentation is to show the great wealth of information that can be gained by laboratory study of a prosimian species that is otherwise difficult to access.

**OBJECT RECOGNITION IN PIGEONS.** *Shigeru Watanabe, Department of Psychology, Keio University, Japan.*

Two groups of pigeons were trained to discriminate 3-dimensional cone and ball using operant conditioning. Real objects were presented to one group while, video images of the objects were presented to the other group. After the subjects accomplished the discrimination task, objects of different size, different orientation or partially occluded objects were presented. The pigeons could recognize larger or smaller objects but could not recognize upside down cone. They did not show clear discriminative behaviour for a triangle made of wood board. These results suggest size constancy but not view point consistency in pigeons. Occlusion of the side half of the cone did not disturb their discrimination but occlusion of the upper or lower half of the objects disturbed the discrimination. The real object group and the video image group showed similar tendency of responding to the test stimuli, although there were some cases of different responding between the real objects and their video images, for example response to the upper half of the ball. Two groups were then tested transfer of discrimination from real to video image or from video image to real objects. They showed transfer of discrimination from real objects to their video images but not from the video images to the real objects.

**COMPARATIVE PSYCHOLOGY: A MODEL FOR THE UNDERGRADUATE CURRICULUM.** *Duncan A. White, Department of Psychology Rhode Island College, U.S.A.*

Although a broad education in the U.S.A. is required for the conventional undergraduate degree, the logic supporting the curriculum is seldom presented to students. Most students view courses in disciplines outside their major as unnecessary time-consuming

requirements for graduation. Modelling comparative psychology's integrative perspective should help students envision the diverse topics taught throughout the curriculum as variations on a common theme. This presentation begins the development of this assertion with a brief review of basic scientific assumptions that are emphasized in comparative psychology. A description of comparative psychology's integrative perspective follows, using Schneirla's levels model as an example. Finally the use of faculty workshops is suggested as a means for implementing a concerted college-wide program designed to daily demonstrate to students the relevance of their interdisciplinary curriculum.

THE USE OF THE GRAIN BEETLE (*Tenebrio Molitor*) TO DEMONSTRATE RESEARCH DESIGN AND BASIC LAWS OF BEHAVIOUR. Duncan A. White, Department of Psychology Rhode Island College, U.S.A.

The purpose of this presentation is to suggest ways to augment present classroom demonstrations and student laboratory investigations and to facilitate comparative education and research. Both the strengths and limitations of *Tenebrio molitor* (*T.m.*) as a classroom and research subject are discussed. Among the useful characteristics of this animal are: (a) the wealth of available information regarding this animal's anatomy, physiology, sensory processing and resultant behaviour; (b) its size and activity level; (c) the ease and inexpense of acquisition, breeding and maintenance in large colonies where space is limited; (d) the fact that *T.m.* is not noxious to the touch or smell, nor is it easily injured by rough handling; (e) its larval, pupal and adult beetle stages of development; and (f) its relatively limited behavioural repertoire and simple biological systems, which aid in the understanding of basic laws of behaviour. *T.m.* can be used to teach students about animal care and ethics in a variety of research designs, from naturalist observations to true experiments. Significant but not daunting limitations to the use of *T.m.* in comparative education and research are (a) methodological issues in the *T. m.* learning literature and (b) the animal's developmental periodicity. Data from classroom demonstrations and research experience of students, colleagues and the presenter are used for elaboration.

THE EMERGENCE OF MODERN COGNITION. *Sarah Wurz, Department of Archaeology, University of Stellenbosch, South Africa.*

Paleolithic archaeology presents us with an unique opportunity to investigate the evolution of human cognition or the modern mind. Changes in life history parameters of *Homo sapiens* ancestors were set in train with the emergence of stone tool technologies and ground dwelling. One of the most important aspects of this process is the enlargement of the brain. Near modern brain capacities were reached by 0.5 million years. Since then there has been selection for the re-organization of the brain and this may have increased the importance of the prefrontal area. Primate morphology and ethology is used to describe the evolutionary circumstances that were driving human encephalisation. The emergence of modern cognition would correlate with a speciation event some 250 000 years ago. It is argued that modern cognition is characterized by the ability to manipulate and communicate in symbols.. Symbolic communication can be traced by symbolic investment in artefact production and products for use in reciprocal exchanges, the use of red ochre as well as the occurrence of distinct regional industries reflecting modern-type linguistic groupings.

# THE NAPOLI SOCIAL LEARNING CONFERENCE

*June 30 - July 5, 1998, Naples, ITALY*

## INTRODUCTION

C.M. Heyes  
*University College London, UK*

B.G. Galef, JR.  
*McMaster University, CANADA*

In 1898, exactly 100 years prior to the Napoli Social Learning Conference, Edward Thorndike published the first experiments investigating whether nonhuman animals are capable of learning by imitation. The results of these experiments, using cats, dogs and chickens as subjects and apparatus of Thorndike's own, somewhat ramshackle construction, housed in Thorndike's own living quarters (Boakes 1984), led him to a strong negative conclusion that was to have a profound effect on the future of comparative psychology. Thorndike inferred from his data that animals, with the possible exception of primates, could not "from an act witnessed, learn to do the act" (Thorndike 1898).

In striking contrast with this image of the young Thorndike as a struggling, isolated, sceptical scholar, the Napoli conference confirmed that, a century later, social learning is a thriving, progressive, international field of enquiry. In the course of five days, researchers from 13 countries, and at least five disciplines (comparative psychology, behavioural ecology, neurobiology, ethology, primatology) gave talks and presented posters indicating that, after a long gestation period, research on social learning has become not only methodologically sophisticated, but also theoretically integrated with a

---

Address correspondence to Dr. Bennett G. Galef, Jr., Department of Psychology, McMaster University, Hamilton, Ontario L8S 4K1, Canada.

number of domains of enquiry concerned with the evolution of both mind and behaviour. The field is formulating important questions, many quite distinct from Thorndike's preoccupations, and arriving at answers that are both clear and of interest to researchers and scholars working in a variety of disciplines.

Two Thorndikean legacies conspicuously apparent at the meeting were the predominance of experimental and comparative methodologies. Indeed, the official title of the conference, "Social learning and cultural transmission: from invertebrates to great apes and humans. Towards a biological synthesis", emphasised its comparative focus. The proceedings included studies from every major class of vertebrates as well as several invertebrate classes. Such comparative emphasis is historically appropriate, as it was Romanes, another turn of the century scholar interested in social learning, who coined the term 'comparative psychology'.

Printed on the following pages are the abstracts of each oral presentation at the Napoli Social Learning Conference. The abstracts appear under four headings: Cognitive mechanisms of social learning; Functional interplay between individual and social learning; Communication; and Roles of social learning in behavioural adaptation.

The papers on cognitive mechanisms, including studies of chimpanzees, rats, marmosets, starlings, capuchins and pigeons, reflected the growing consensus that "two-action" tests are the most effective means of demonstrating and analysing imitation learning in nonhuman animals. At their strongest, these procedures control for non-imitative varieties of social learning (e.g. stimulus/local enhancement, social facilitation, emulation, observational conditioning) by contrasting the performance of 'observers' that have seen single objects manipulated by a 'demonstrator' (conspecific or human) using different appendages and/or response topographies. Work with this method has indicated that a range of species can imitate.

Current research investigates the degree to which imitative performance reflects cognitive complexity by examining whether animals can acquire by observation information about 'novel' behaviour, and the serial order of actions (Heyes, Huber, Whiten, Zentall). Other contributors in this section argued compellingly that the distinction between individual and social learning has been over-emphasised (Visalberghi, Frigaszy & Galloway), and that associative learning theory has substantial heuristic potential in the investigation of both psychological and neurobiological mechanisms of social learning (Frigaszy, Ray & Heyes).

Consistent with the idea that common mechanisms underlie individual and social learning, papers in the second section reported evidence of social learning in every invertebrate class (Fiorito & Webster; Traniello) and data showing that capacities for individual and social learning are highly correlated within and across a range of bird species (Lefebvre). However, the papers in this section were primarily concerned, not with mechanism, but with the functional interplay between individual and social learning and the ecological variables favouring each. Giraldeau proposes a general framework for research in this area, incorporating a taxonomy of levels of social learning, experimental methods and mathematical modelling techniques. Other contributors, using such modelling techniques (Best) combined with experiments on replicate populations of guppies (Laland, Reader & Laland), provided evidence that the benefits of social learning depend on reproductive strategies, the individual's potential to innovate, and, more generally, the degree to which a species' adaptive landscape permits 'deviation' from the socially-transmitted norm.

Oral presentations concerning communication were as varied as is the topic itself. Both Freeberg, King and West and Gajdon and Stauffacher focussed on the role of social interaction between naive and knowledgeable animals in determining what is communicated. While Gajdon emphasised the importance of understanding the behaviour of the tutor and possible insights that study of 'coaching' might play in understanding animal imitation, Freeberg focussed on the necessity of examining the structure of social interactions to determine where, when and how social learning occurs. Gardner described parallels in the spontaneous acquisition of models' behaviour by infant humans and chimpanzees, while Schuster described studies of cooperative behaviour in animals and their potential contribution to the field. Last, but certainly not least, Susswein reviewed an elegant series of studies of the effect of chemicals released by conspecifics on feeding behaviour and learning and memory processes in *Aplysia*.

Papers on the functional significance of social learning were equally varied. Ribes-Inesta introduced a Wittgensteinian conceptualisation of cultural learning in humans. The role of social learning in feeding and nest material choice by rabbits (Altbacker & Bilko), in choice of a sexual partner by Japanese quail (Galef & White), and selection of medicinally active plants by African great apes responding to illness (Huffman) each received attention. Perhaps most striking was Huffman's report of painstakingly collected field data indicating local and regional traditions in chimpanzees in the plants

they select for ingestion when ill.

The Napoli Social Learning Conference was sponsored by the Stazione Zoological 'A. Dohrn' di Napoli, Istituto Italiano Studi Filosofici, Association for the Study of Animal Behaviour, CNR, and Eppendorf s.r.l. (Milano). All those who attended are grateful to Graziano Fiorito and his organising committee: Louis Lefebvre; PierGiorgio Montarolo; Emanuela Prato-Previde; Paola Valsecchi; Elisabetta Visalberghi; and Andrew Whiten.

## REFERENCES

- Boakes, R. (1984) *From Darwin to Behaviourism: Psychology and the Mind of Animals*. Cambridge: Cambridge University Press.
- Thorndike, E. L. (1898) Animal Intelligence: An Experimental Study of the Associative Processes in Animals. *Psychological Review, Monograph Supplement No. 8*, 68-72.



## THE NAPOLI SOCIAL LEARNING CONFERENCE *June 30 - July 5, 1998, Naples, ITALY*

### ABSTRACTS OF PAPERS

#### COGNITIVE MECHANISMS

THE TIES THAT (MIGHT) BIND. *D.M. Frigaszy, Psychology Department, University of Georgia, Athens, USA.*

Can social learning and neurobiology be combined meaningfully in the same sentence? That depends on what the conversation is about. Social learning, to paraphrase L.-A. Giraldeau, is learning about the value of events, objects, or alternative courses of action, or learning how to achieve certain goals, from public information provided by another. Behavioral biologists distinguish social learning from other forms of learning by the source of information and perhaps the form of information (in the case of actions), but not the nature of the learning process. As B. Galef has pointed out many times, unless one posits a new mechanism of learning not yet imagined by neurobiologists or learning theorists, the same mechanisms (here, the same neural machinery and processes) must of necessity mediate all forms of learning, social and otherwise, in the individual.

Neurobiologists examine the ways neural systems work to achieve functional outcomes for the organism. Neurobiological models of learning span many levels of explanation, from the properties of receptors and membranes, to cell structure organization and patterned activity of circuits or regions. Can social learning be studied meaningfully at the levels of interest to the neurobiologist? Perhaps. It will be most interesting for both behavioral and neurobiologists if it can be. However, claiming something special for social learning at these levels requires distinguishing between social learning and "normal"

---

The e-mail addresses of corresponding authors and the titles of the 53 posters presented at the Napoli Social Learning Conference, organised phylogenetically according to subject species are available at the following Web site:

<http://alpha.szn.it/~gfiorito/social.htm>

(asocial) learning. This can be done *only* if there is some detectable and functionally significant difference (at the neural level) between socially provided information and information gained in other ways, as this is the only difference between social learning and asocial learning at the level of the organism. No such differences have yet been proposed, to my knowledge. In my view, if they exist, we are most likely to find them (first) in the organization of patterned activity, as it is the phylogenetically more diverse level of neurobiology, and social learning varies considerably across genera in its likelihood and manifestations.

Drawing from a comparative psychologist's selective familiarity with current neurobiological thinking, I will suggest why socially provided information may differ from other forms of information at the level of patterned activity within and across brain regions or circuits. Perhaps the neurobiologists in the audience will have views on the likelihood of such differences, or will have others to suggest, or ideas about how postulated differences might be identified empirically. Although it is too early for a productive synthesis of the neurobiology of learning and social learning, it is not too early to consider the merits of such a project together. Let the conversation begin!

**SOCIAL VERSUS INDIVIDUAL LEARNING: SIMILARITIES AND DIFFERENCES.** *E. Visalberghi<sup>1</sup>, D. Frigaszy<sup>2</sup> and A. Galloway<sup>2</sup>, <sup>1</sup>Istituto di Psicologia, CNR, Roma, Italy, <sup>2</sup>Psychology Department, University of Georgia, Athens, GA, USA.*

In the last few years, social learning has been the focus of renewed interest. We welcome this interest, but are concerned about three major weaknesses in current research. 1) The surge of newly published definitions of social learning phenomena often lack operational criteria. This is problematic for comparisons across species and especially across higher taxa. 2) The biological significance of social learning is not always an initiating focus of research. This is unsatisfactory for behavioral biologists, who, we believe, represent the majority of social learning researchers. Difficulties in interpreting social learning from an evolutionary or comparative standpoint may be overcome by developing metrics of the potential fitness consequences of social learning. For example, biological significance might be measured by the time an individual requires to learn X, or by the rate of transmission of X in a group. Other proposed measures of biological significance examine what is learned, and direction of behavior transmission. 3) Claims that social learning is unique or special in process or outcome are often accompanied by inadequate evidence.

To illustrate these points, we will consider the status of operational definitions, and evidence of both the biological significance and putatively unique properties of documented social influences on feeding. Through the analysis of literature on human and nonhuman primates, domesticated species, birds, and rodents, we will explore whether the initiation of consumption or selection of foods is affected by the feeding activity or food choices of conspecifics.

**TRANSFORMATIONAL AND ASSOCIATIVE THEORIES OF IMITATION.** *C. M. Heyes, Department of Psychology, University College London.*

Actions vary on a dimension of perceptual opacity. Perceptually transparent actions give rise to similar patterns of sensation when observed and executed, while perceptually opaque actions yield sensory input in different perceptual frames and/or modalities when observed and executed.

The most significant challenge for any theory of the psychological mechanisms of imitation is to explain reproduction of perceptually opaque actions. Theories that have tackled this problem in the last century are of two kinds: Transformational theories suggest that complex (and largely unspecified) operations are performed on sensory input from the model, recoding it for motor output. In contrast, associative theories claim that mapping between sensory input from the model and motor output is achieved on the basis of correlated experience of observing and executing actions or action components.

An Associative Sequence Learning (ASL) model of imitation will be used as a contemporary example of a theory of the latter kind, and it will be argued that the importance of research on imitation of perceptually opaque actions in infants and nonhuman animals lies in its potential to provide evidence favouring transformational over associative theories of imitation.

**UNDERSTANDING THE EMERGENCE OF NOVEL FORMS IN IMITATIVE LEARNING.** *Ludwig Huber, Bernhard Voelkl and Sabine Rechberger, Institute of Zoology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria.*

The artificial-fruit method was used in a comparative study of movement imitation in marmosets (*Callithrix jacchus*) and keas (*Nestor notabilis*). Regardless of whether the animals had any insight into the causal structure of the foraging problem, they faithfully reproduced the observed technique; solving the problem both faster and with fewer

errors than did control groups not exposed to a demonstrator.

Novelty is commonly used as a cardinal requirement for both insightful imitation and slavish copying. However, neither the learning process nor the experimental analysis allows emergence of novel patterns of behaviour to be identified in an all-or-none fashion. Rather, assimilation and accommodation of functional behavior, during which novel forms emerge, is based on a dynamic process of neuronal reorganization. Consequently, a conceptual shift is required to describe both the effects and the processes of imitative learning. This could be achieved through use of a dynamic systems approach. There is also a need for improved methods for dissecting the mechanisms underlying imitation. This was attempted by employing sophisticated video analysis techniques and mathematical descriptions of movement; the first results of which are presented here.

IMPLICATIONS OF CONTEMPORARY LEARNING THEORY FOR SOCIAL LEARNING RESEARCH. *E. D. Ray and C. M. Heyes, Department of Psychology, University College London, UK.*

It has been assumed that the formation of S-R links, whereby stimuli previously experienced contiguously with the execution of a response come to elicit that response, is either sufficient to explain social learning or, particularly in the case of observational learning, that it is inadequate to do so. Contemporary learning theory conceives of learning rather differently; as the formation and association of mental representations. It is argued that the problems which affected learning theory in the behaviourist era are those which arise in trying to understand social learning today. Therefore, social learning theory might similarly benefit by understanding learning to involve the cognitive processes that contemporary associative learning theory proposes. Conceiving of learning as the acquisition of information has many theoretical and empirical implications for social learning research and these will be illustrated by reinterpreting effects documented in the literature and data from new experiments. For example, a cognitive social learning theory acknowledges that the ability to learn about stimuli confers considerable behavioural flexibility, casts observational conditioning as a functionally important and pervasive social learning process, and suggests that social learning is likely to result in conditioned responses other than matching behaviour. A cognitive social learning theory also predicts the occurrence of socially mediated inhibitory learning.

COGNITIVE ISSUES IN IMITATION. *Andrew Whiten, Scottish Primate Research Group, School of Psychology, University of St Andrews, UK.*

To date, the objective of most imitation research has been simply to establish whether the phenomenon exists in the species studied: relatively little work has explicitly addressed questions of underlying cognition. This applies even to the case of imitation, which is understood to involve a distinctive, but largely unspecified, type of cognition. In this paper I consider a series of cognitive issues in the study of imitation. Empirical material comes principally from new studies of the imitation of "artificial fruit" processing in chimpanzees. The issues analysed are: 1) Copying sequential structure; 2) Copying hierarchical structure; 3) Imitation versus emulation; 4) How novel acts are imitated; 5) The nature of feedback in imitation; 6) Existence of a concept of imitation; 7) The role of imitation in culture; and 8) The role of enculturation in imitation. Empirical results now cast some light on nearly all of these, but the aim of the presentation is also to highlight gaps in our knowledge and discuss possible ways of filling them.

THE SEARCH FOR A THEORY OF IMITATIVE LEARNING IN ANIMALS. *Thomas R. Zentall, University of Kentucky, USA.*

The recent publication of refined demonstrations of imitative learning in a variety of species has led to renewed interest in understanding the mechanisms responsible for this behavior. Imitative learning has been explained by developmental psychologists either in terms of simple learning principles (e.g. instrumental learning), or in terms of complex cognitive principles (e.g. perspective taking). Research suggests that simple learning principles are insufficient to account for imitation. Furthermore, many animals that appear to be capable of imitative learning show little evidence that they are capable of perspective taking, or even mirror-image recognition, proposed by some to underlie perspective taking. Biologists, on the other hand, tend to view the various forms of social learning, including imitation, as genetically predisposed. However, predispositions of the type generally proposed (e.g. contagion) are unlikely to account for the relatively arbitrary nature of behaviour that can be imitated. Although it is likely that imitative learning has been evolutionarily selected in certain species because it allows for rapid behavioural plasticity without the need to suffer the consequences of 'trial and error learning', such an account does little to clarify its underlying mechanisms. An adequate theoretical account of imitative learning in animals remains a challenge to researchers in the this field.

## FUNCTIONAL INTERPLAY BETWEEN SOCIAL AND INDIVIDUAL LEARNING

### GENES, INDIVIDUAL LEARNING, AND SOCIAL LEARNING.

*Michael Best, Massachusetts Institute of Technology, Media Laboratory, Cambridge, MA, USA.*

We studied the relationship between genes, individual learning, and social learning. We started with the simulation environment of Hinton and Nowlan in which individual learning was shown to guide organic evolution towards a difficult adaptive goal. We add to this environment "culture" in the form of social learning via imitation.

Our results demonstrate that when genes and culture cooperate, or enhance one another, culture is able to guide organic evolution towards an adaptive goal. Further, we show that social learning is superior to individual learning insofar as it converges more quickly on the goal than does individual learning. However, the social-learning algorithm results in slower genetic assimilation of adaptive alleles than does individual learning. It is as if, we argue, adaptive values are stored in culture rather than in genes. Finally, we consider when culture and genes pursue diametrically opposed goals. We show that when the two algorithms are opposed, culture, in the form of social learning, is no match for organic evolution with individual learning. In fact, only the most Herculean of social learning algorithms is able to keep a neutralizing toe-hold against the slow, plodding force of organic evolution. Our results suggest that both when in opposition and in agreement, transmission forces, such as the ratio of teacher to learner, are central to the success of social learning. Finally, in new results, we consider the relative force of horizontal, vertical, and oblique transmission modes.

### WHEN IS SOCIAL LEARNING ADAPTIVE? *K.N. Laland and K. Williams, Sub-Department of Animal Behaviour, University of Cambridge.*

Social learning is clearly an important adaptation that allows animals to acquire information about their local environments rapidly, efficiently, and at low cost. Moreover, socially acquired information is typically expressed in adaptive behaviour. However, in a changing and variable world, theoretical models suggest that social learners risk picking up outdated or inappropriate information. This talk brings together theoretical and empirical insights to discuss the circumstances under which social learning is adaptive.

In order to fully understand the adaptive significance of social learning distinctions must be made between: (1) the capacity for social learning, (2) the behaviour of an individual influenced by, or resulting from, social learning, (3) the socially acquired information, and (4) the behavioural tradition. Theoretical models have shed light on the circumstances under which a capacity for social learning would or would not be favoured by natural selection. Human learned behaviour is frequently maladaptive, but this is rarely the case for animals, and the difference can be understood in light of findings from evolutionary models. However, animals may frequently acquire and express maladaptive information, and may maintain maladaptive traditions.

What constitutes adaptive behaviour for an individual depends on the behaviour of others. Transmission chain experiments on the social learning of foraging information in guppies provides empirical support for this position. It is concluded that selectively neutral and sub-optimal behavioural alternatives may be maintained as short-term traditions in animal populations.

THE COMPARATIVE ECOLOGY OF SOCIAL LEARNING. *Louis Lefebvre, Department of Biology, McGill University, Montreal, PQ, Canada.*

Comparative studies have identified three types of learning characterized by a robust association between neural substrate, evolutionary co-variables and readiness to learn: parental imprinting, song imitation and spatial memory. Attempts to apply this comparative logic to social learning have produced disappointing results: (1) ecologically-correlated differences in social learning do not appear to be specialized; they also extend to individual learning; (2) intervening variables, like neophobia and tameness, co-vary with differences in learning; (3) ecologically-correlated learning differences may be learned, and not due to divergent natural selection. Similar problems occur if we look at the overall link between learning and the exploitation strategy most logically associated with it, opportunistic generalism. One solution is to bypass captive learning experiments altogether and to test directly in the field the predicted link between opportunistic generalism, neural substrate, and developmental costs. Three new ways to operationalize and quantify opportunistic generalism will be presented: rate of feeding innovations, use of modified habitats, and pair-wise prediction matrices. Field and laboratory reports of social learning could be treated in a similar comparative way, without regard for mechanistic distinctions, in a search for broad evolutionary correlates, either phyletic or ecological.

**SOCIAL LEARNING: A BEHAVIOURAL ECOLOGICAL APPROACH.** *Luc-Alain Giraldeau, Department of Biology, Concordia University, Montreal, PQ, Canada.*

Learning requires the use, processing, storage and retrieval of information. This information can be used to learn about the value of alternative courses of action or to learn how to accomplish certain tasks. In the context of foraging behaviour, for instance, "learning about" may involve estimating the value of alternative prey types while "learning how" involves acquiring the skills required to handle, find or uncover each prey type.

The information upon which learning how or about depends can come from either of two sources. In one instance, the information originates from an individual's personal transactions with the environment leading to individual, non-social learning. Information can also originate in transactions of other individuals with the environment. Such information is public, in the sense that it is available to all. Social learning involves instances of learning based on the use of public information.

I review instances of social learning how and about, and propose a functional classification of social learning how into three categories: area copying, object copying and behaviour copying. I review some adaptive hypotheses for each, and propose that future studies should investigate the conditions under which these forms of learning are used.

**INVESTMENT ASYMMETRIES, INNOVATION AND THE SOCIAL TRANSMISSION OF INFORMATION.** *Simon Reader and Kevin Laland, Sub-Department of Animal Behaviour, University of Cambridge, UK.*

Theoretical models of the social transmission of information have tended to neglect the effects of differences in the abilities or propensities of individuals to innovate and learn from others. Evidence from the guppy (*Poecilia reticulata*) suggests that the sex, size and motivational state of an individual can strongly bias both the likelihood that an individual will innovate and the spread of such novel behaviour patterns. We propose that this may be the result of parental investment asymmetries and differences in competitive ability. Since such asymmetries are common to many vertebrate species, similar effects may be widespread and may help to explain why relatively few innovations appear to spread in the wild.

Mathematical models predict that the cumulative number of individuals displaying a novel behaviour will follow a sigmoidal pattern



over time. A sigmoidal diffusion curve may also result from individual variation in asocial learning. However, analysis of the diffusion curves in replicate experimental populations of guppies found the hyperbolic sine function provided the best fit. It is likely that both asocial and social learning processes were operating in these experimental populations. To understand fully the dynamics of information flow, it may be necessary for models to allow for the dual processes of individual and social learning.

**THE ECOLOGY AND EVOLUTION OF INDIVIDUAL AND COLONY LEARNING IN ANTS.** *James Traniello, Boston University, Department of Biology, Boston, Massachusetts 02215, USA.*

Dividing labor and scheduling tasks such as brood care and foraging according to worker morphology and age has historically been regarded as an example of the programmed simplicity of worker behavior in social insects, such as ants. Recent research, however, has shown that behavior changes adaptively in response to individual experience and the social environment. Task specialization, which is achieved through programmed behavioral development and learning, is thought to improve the efficiency of individual labor and thus colony fitness. Foraging efficiency, for example, has been shown to increase with individual experience in seed-harvesting ants, and individual and colony-level learning and memory appear to be adaptive. Also, colonies of leaf-cutter ants show conditioned feeding responses that are based upon the foraging decisions of scouts that locate new sources of leaves. Additionally, learning at the colony level may concern the recognition of and social response to neighbouring and competing ant species.

Studies of the search behavior of the ant *Formica Scyphozoa* show that worker task specialization and learning ability appear to be influenced by the distribution of food resources in time and space. Resources with different distributions (protein and carbohydrate food) elicit individual search responses that appear to enhance foraging efficiency. In particular, workers tend to concentrate their search effort close to the site of a prior carbohydrate, but not a protein, food load. Resource-related search behaviors appear to be innate and workers cannot be conditioned to increase area-restricted search behavior using consecutive rewards of protein food. Ecology, therefore, seems to set limits on individual learning ability. However, individual ants may increase food collection by stimulating other individuals to forage.

Considering the phylogeny and sociobiology of ants as a whole,

there appears to be an inverse relationship between the degree of social complexity and individual learning ability. Collective action, mediated by chemical signals, may compensate socially for limits on individual learning ability in ants.

**A REVIEW OF SOCIAL LEARNING PHENOMENA IN INVERTEBRATES.** *Sandra J. Webster<sup>1</sup> and Graziano Fiorito<sup>2</sup>, <sup>1</sup>Department of Biological Sciences, McGill University, Quebec, Canada; <sup>2</sup>Laboratorio di Neurobiologia, Stazione Zoologica 'Anton Dohrn', Napoli, Italy.*

Most of the current literature on social learning focusses on vertebrate species. This paper reviews evidence of social facilitation and/or social learning in invertebrates. Our principal goals are to increase awareness of social learning phenomena in invertebrate groups, ranging from the simple *Planaria* to molluscs and arthropods, and to modernise their scientific interpretation. We will emphasis contrasts between the original interpretative frameworks and our contemporary view, and we will propose a potential "model" preparation for the investigation of invertebrate social learning.

## COMMUNICATION

**PROBING THE DEEP STRUCTURE OF SOCIAL EXPERIENCE: STUDIES OF THE DEVELOPMENT OF COMMUNICATING.** *T.M. Freeberg, A.P. King and M.J. West, Department of Biological Sciences, Purdue University, West Lafayette, IN 47907, USA; Department of Biology and Psychology, Indiana University, Bloomington, IN 47405, USA.*

Studies of the role of social learning in the development of avian communication have typically uncovered only the surface structure of social influences. Here we argue for probing deeper structures of social influences in studies of effects of social experience on vocal development and, more generally, in studies of social learning in animals. Traditionally, both "endpoint" and developmental studies of vocal ontogeny have focussed solely on the vocal signal itself. We believe researchers must broaden their focus to include the development of communicating, of which vocal signals are but one part. Assessing the development of communicating with the goal of elucidating the deeper structures of social experience requires that we study the very social interactions that induce, facilitate, and/or maintain

communicative competence in individuals. Study of these social interactions requires intensive analyses of individuals while communicating both as signallers and as receivers within their social group. Such analyses are no small task. However, we present data from previous and ongoing work with Brown-headed Cowbirds (*Molothrus ater*) indicating that documenting deeper structures of social experience is absolutely necessary for full understanding of how, when, and perhaps why, social influences affect the development of both communication and communicating.

SHIFTING ATTENTION FROM QUESTIONS CONCERNING NAIVE ANIMALS TO QUESTIONS CONCERNING TUTORS- A NEGLECTED TOPIC IN SOCIAL LEARNING? GK. Gajdon and M. Stauffacher, Swiss Federal Institute of Technology ETH, Institute of Animal Sciences INW, Schwerzenbach, Switzerland.

Most studies in social learning focus on the bystander side of the bystander-tutor system. Research is, to a great extent, concerned with the cognitive level on which one animal learns from another. Tutors constitute an alternative, yet equally important, topic. Neglect of the role of the tutor in social learning is reflected in the fact that few studies are concerned with teaching. Examining corrective intervening behaviour ('coaching') suggests that there might be a link between limited knowledge of this form of teaching and the paucity of evidence for imitation. Common to both imitation and coaching is comparison of one's own behaviour with the perceived behaviour of a conspecific .

Lack of evidence for imitation seems to reflect an insensitivity to details of the performance of others. Why then should animals show such a sensitivity when coaching others? In fact, evidence of coaching is rare in animals. Research to determine whether animals even recognize a companion's mistakes would help to understand the lack of evidence of coaching. Further, if even animals that already know a behaviour pattern don't recognize divergence in the same behaviour pattern in other animals, evidence would be provided that imitation exceeds the animal's cognitive abilities. Another question is: What characteristics define the most effective tutors for which class of bystanders? Once best tutors are defined, experiments using such elite tutors, as well as especially competent bystanders may improve our understanding of the range of social learning abilities in animals.

THE FUZZY LOGIC OF SOCIAL LEARNING. *R. Allen Gardner, University of Nevada, USA.*

Human children incorporate adult routines into their developing repertoires. Incorporation is usually partial and often fragmentary. Precise replication is unnecessary, often impossible, and probably unwise. Incorporation appears throughout ethology. Young birds must hear adult songs, but only incorporate elements into their own developing repertoires. Chimpanzees, cross-fostered in human homes, begin by incorporating fragments of adult routines. The chimpanzees' routines develop in a pattern much like that seen in human development. For example, after observing adults sweeping, infant chimpanzees, like children, begin by riding on the broom as an adult sweeps the floor or by helping to push the broom. Gradually, the chimpanzees and children develop into effective sweepers and work independently at the task. This paper focuses on a pattern of incorporation and expansion that fits the fuzzy logic of modern science better than the Aristotelian tradition of logic-tight categories.

THE COOPERATIVE BEHAVIOR OF DYADS. *Richard Schuster, Department of Psychology, University of Haifa, Israel.*

Many species engage in a type of cooperation, often termed mutualism, whereby individuals learn to coordinate behaviors for joint outcomes. According to theories in evolutionary biology, psychology and game theory, cooperation is expected when individuals experience more favorable outcomes when cooperating than when behaving alone. Field studies of mutualisms, however, sometimes fail to confirm that all participants benefit, raising questions about why and how animals cooperate. Our research asks whether part of the answer resides in social relationships and their consequences that cannot be addressed with experimental designs using animal or human subjects that minimize social interactions by isolating subjects in separate chambers. Using laboratory rats, pairs are rewarded for coordinating movements within a shared chamber. Coordination strategies emerge that typically incorporate asymmetries expressed in aggressive dominance, initiation of interactions, and division of obtained outcomes. These dyadic relationships influence the roles adopted by cooperators, the attractiveness of outcomes, competition over outcomes and choice between cooperation and individual action. We will be examining within-pair differences in physiological states associated with these asymmetries. More generally, this research addresses the design of laboratory paradigms appropriate for studying why and how cooperative behavior varies across individuals, sex, age and species.

**SOCIAL STIMULI AFFECT MANY ASPECTS OF LEARNED AND UNLEARNED BEHAVIOR IN APLYSIA FASCIATA.** *A.J. Susswein, M. Schwarz, S. Blumberg, M. Levy, I. Ziv, T. Haran and S. Markovich, Department of Life Sciences, Bar Ilan University, Ramat Gan, Israel.*

*Aplysia fasciata* are highly social animals. They sense one another's presence via the chemosensory rhinophores, which respond to pheromones affecting many behaviors. A number of peptides thought to be pheromones are synthesized and released from various tissues in the reproductive tract. *Aplysia* react differently to newly introduced individuals and to individuals to which they have been previously exposed, suggesting that they can distinguish novel and familiar conspecifics. One effect of pheromones is to facilitate feeding behavior. Pheromones also modulate performance in an instrumental learning task affecting feeding. In this task, animals stop responding to a palatable food which is too tough to eat. Long-term memory is shown by a decreased responsiveness 24 hours after training. Isolating animals from conspecifics during training obstructs learning, and isolating them for an hour after training blocks long-term memory. The effects of isolation are reminiscent of the modulation of learning and memory by trauma or stress in vertebrates, suggesting that social isolation in *A. fasciata* may be an analog of stress. In mammals, stress-evoked modulation of memory is affected by a number of modulatory neurotransmitters. These transmitters also modulate the neural circuitry controlling *Aplysia* feeding. Many neurons initiating and organizing *Aplysia* feeding are identified, opening the possibility of examining the physiological basis of how social stimuli affect learning and memory.

## ROLES OF SOCIAL LEARNING IN BEHAVIOURAL ADAPTATION

**FOOD PREFERENCES IN THE EUROPEAN RABBIT: LONGEVITY, DURABILITY AND ECOLOGICAL SIGNIFICANCE OF SOCIAL LEARNING.** *V. Altbacker and A. Bilko, Department of Ethology, Eotvos University, Hungary.*

We have previously demonstrated that a rabbit mother's diet can influence her pups' food preferences at weaning. Supplementing a mother's diet during pregnancy and lactation with either 10% juniper berries or thyme leaves resulted in preference for that plant when weanling animals were tested in a three-choice situation. However, there was a rapid decrease in preference, presumably as a consequence of eating the less-nutritious, aromatic plants. We determined whether this decrease could be prevented by reducing the amount of aromatic

compounds eaten by pups. Durability of preference was studied by delaying the test. Pups of both juniper-fed and control mothers were tested for only 2 h/day, and some tests were postponed 1 week, 1 month or 6 months after weaning. We found a significant, long-lasting juniper preference in all treated pups, even those tested 6 months after their last exposure to juniper. These findings indicate that weaned rabbits might use mother-mediated information concerning edible foods for several seasons. We also tested whether such social learning affects food choice of wild rabbits. We collected newborn rabbits from the wild and cross-fostered them to females in the laboratory that we fed lab chow. These cross-fostered pups preferred juniper berries after weaning. Other pups, either taken from habitats without juniper or born in the laboratory to lab-chow fed mothers, showed no preference for juniper except when cross fostered to juniper-fed mothers. Thus, the previously demonstrated social learning might be a key factor in development of independent feeding and result in traditions of diet selection in wild rabbit populations.

**SOCIAL EFFECTS ON MATE-CHOICES OF MALE AND FEMALE JAPANESE QUAIL, *COTURNIX COTURNIX JAPONICA*.** *Bennett G. Galef, Jr. and David J. White, Department of Psychology, McMaster University, Hamilton, Ontario, Canada.*

For the past 2 years, my laboratory has been examining social influences on the mate choices of both male and female Japanese quail. We have found that: (1) female quail increase their tendency to affiliate with males they have seen mating with other females, (2) male quail decrease their tendency to affiliate with females they have seen mating with other males, and (3) in both male and female quail affiliative preference correlates with copulatory preference; i.e. both male and female quail prefer to remain close to individuals with whom they will copulate when given the opportunity.

Our analyses of the behavioural processes enhancing females' tendencies to affiliate with males seen mating with other females reveals that both 'conspecific cuing' and something like 'mate-choice copying' play a role in altering the mate choices of observing females. However, attempts to demonstrate that females truly 'copy' the mate choices of other females by eliminating alternative explanations of correspondence in behaviour, like attempts to demonstrate true 'imitation' of motor patterns in animals in the same way, seem unlikely to be successful. There are lessons to be learned from the 100-year history of the study of learning by imitation, that should help us to avoid pitfalls in analyses of social influences on mate choice.

THE RELATIVE CONTRIBUTIONS OF BIOLOGICAL PREDISPOSITIONS, SOCIAL LEARNING, AND ECOLOGY IN THE TRANSMISSION AND MAINTENANCE OF BEHAVIORAL TRADITIONS. A CASE STUDY OF SELF-MEDICATIVE BEHAVIOR IN AFRICAN GREAT APES. *Michael A. Huffman, Kyoto University, Primate Research Institute.*

Despite many recent advances in social learning theory, little is known about the relative roles of biological and ecological factors in socially mediated transmission and maintenance of behavioral traditions in nature. Two forms of self-medication in great ape species (bitter pith chewing and leaf swallowing) have been noted in a number of populations across Africa and are hypothesized to aid in control of parasitic infections (Huffman, 1997). Effects of parasitosis on hosts' behavior and reproductive fitness are great. Consequently, predispositions to 'recognize' cues both pertaining to pharmacological activity and for unusual ingestive patterns are probably products of natural selection, and are likely to play an important role in the expression of self-meditative behavior. The diversity of plant species selected by apes in different areas is influenced by ecological and geographical factors, yet all apes display common selection criteria and behavioral patterns. Within groups, however, social learning processes important in maintaining plant species preferences are propagated both between mother and young and among adults.

Neighbouring groups select many of the same and/or similar species for both bitter pith chewing and leaf swallowing, resulting in localized and regional traditions. These local behavioral traditions are probably maintained by information exchange via female transfer. These details will be discussed, and a model proposed for the origins, mechanisms, and learning processes of self-medication.

CULTURAL ADJUSTMENT AND SOCIAL LEARNING VIEWED FROM THE PERSPECTIVE OF CRITERIA AND LANGUAGE-GAMES. *Emilio Ribes-Inesta, University of Guadalajara, Mexico.*

The human environment is, by definition, cultural. The environment of human behavior consists mainly in constructed objects and conventions. On the same token, human behavior consists in learned responses adjusted to those objects and conventions. Since conventions involve the shared practices of the individuals pertaining to a given social group, the adjustment of human behavior is always prescribed by various criteria, either explicitly or implicitly present in the performance of various social practices. Human social learning is





## Instructions to Authors

All manuscripts are reviewed by two readers other than the Editors. Authors should send three copies of their manuscripts to one of the Editors. One diskette copy saved in ASCII format or as a standard word processor file, will need to be submitted to the Editor once the manuscript is accepted for publication. Electronic versions of figures are also preferred at this stage. Indicate clearly on the diskette the author(s) name(s), file format and program version number. (Alternate arrangements may be possible for those authors who are unable to provide a diskette copy).

The manuscript should have a cover page with the full title, the author(s) name(s) and address(es) and should indicate the person with whom the Journal may correspond. If the author(s) has(ve) an electronic mail address or fax number, these should be given in a cover letter accompanying the manuscript. The abstract should be on a separate page. All articles are published in English; the author(s) should also submit an abstract in their language if it does not require non-Roman type. Author(s) are responsible for the accuracy of the non-English abstract. Acknowledgements should appear on a separate page and carry the title of the article and the author(s) name(s). If the author(s) prefer(s) anonymity in the review process, this should be stated in a covering letter and the manuscript, abstracts, and illustrative material should carry only the title of the article. The cover sheet and acknowledgements will not be sent to the reviewers in this instance.

**GENERAL REQUIREMENTS** Logical organization is essential. While headings help to structure the content, titles and headings within the manuscript should be as short as possible. Tables and figures should not be redundant. Illustrative material should be self-explanatory and used sparingly. Tables and figures must be in camera-ready condition and include separate captions. Labels on figures should be either Helvetica or Times Roman font and be sufficiently large to allow clarity when reduced. Black and white shading is preferred to more complex fill patterns. Electronic versions of all figures should be included on the final submitted diskette if possible. Only items cited in manuscripts should be listed as references. Page numbers must be provided for direct quotations. Footnotes should not be used except in special circumstances and with permission of the Editor.

**MANUSCRIPTS** should be double-spaced, the original on white bond paper, with margins of 3 cm on all four edges and approximately 26 lines to the page. Manuscripts longer than 20 typed pages (not counting figures, tables, and references) will only be considered in unusual circumstances. The current style manual of the American Psychological Association is to be followed. Manuscripts which do not meet the style requirements will be returned for retyping.

**REFERENCES** should be listed on a separate page and referred to in the text by author(s) and year of publication as in the Publication Manual of the American Psychological Association.

